CLASSIFICATION, PHYLOGENY, AND ZOOGEOGRAPHY OF *HYDATICUS* LEACH (COLEOPTERA: DYTISCIDAE) OF NORTH AMERICA[1]

R.E. Roughley
Department of Entomology
University of Alberta
Edmonton, Alberta, Canada
T6G 2E3

D.H. Pengelly
Department of Environmental Biology
University of Guelph
Guelph, Ontario, Canada
N1G 2W1

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ABSTRACT

The five Nearctic species of Hydaticus *Leach are assigned to the subgenera* Guignotites *Brinck and* Hydaticus sensu stricto. *These are* H. (H.) modestus *Sharp, 1882 (=*H. rugosus *Poppius, 1905 new synonomy; type area– Ust Aldan, U.S.S.R.),* H. (H.) piceus *Lecönte, 1863, and* H. (H.) cinctipennis *Aubé, 1838 which is recognized as a valid taxon. The Nearctic species of* H. (Guignotites) *are* H. (G.) rimosus *Aubé, 1838 and* H. (G.) bimarginatus *(Say, 1831). Because of the similarity between* H. rimosus *(type not located) and* H. bimarginatus *a neotype is designated for* H. bimarginatus *from the LeConte collection. All of these taxa are keyed, diagnosed and described in terms of morphological features of adults, geographical distribution and habitat.* Hydaticus riehli *Wehncke, 1876 (type area--Cuba) is considered to be a species of uncertain placement.*

A reconstructed phylogeny of genera and subgenera of Hydaticini indicated that this tribe is comprised of two genera: Hydaticus *Leach and* Prodaticus *Sharp; and that* Hydaticus *includes the subgenera:* Hydaticus (s. str.), Guignotites *Brinck,* Hydaticinus *Guignot, and* Pleurodytes *Régimbart, new status. The reconstructed phylogeny of Hydaticini and the species group of* Hydaticus s. str. *which includes Nearctic species is used in conjunction with other features of these taxa to construct an hypothesis accounting for the differentiation and distribution of these taxa. The hypothesis is that the ancestral stock of Hydaticini is of gondwanian origin, and that present-day Africa has been a zoogeographic centre from which taxon pulses have originated. The Nearctic* Hydaticus *fauna is comprised of three separate colonizations of North America: via a North Atlantic land bridge (ancestral stock of* H. piceus-H. cinctipennis*) via Central America after a closure of the Panamanian portal (ancestral stock of* H. modestus*). Subsequent vicariance of the two ancestral stocks has produced the present pattern.*

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RÉSUMÉ

*Les cinq espèces d'*Hydaticus *néarctiques sont assignées aux sous-genres* Guignotites *Brinck et* Hydaticus sensu stricto. *Ce sont:* H. (H.) modestus *Sharp, 1882 (=* H. rugosus *Poppius, 1905, synonyme nouveau; région typique– Ust Aldan, U.R.S.S.),* H. (H.) piceus *LeConte, 1863, et* H. (H.) cinctipennis *Aubé, 1838, cette dernière espèce étant reconnue comme valide. Les espèces néarctiques d'*H. (Guignotites) *sont* H. (G.) rimosus *Aubé, 1838 et* H. (G.) bimarginatus *(Say, 1831). Etant donné ressemblance entre* H. rimosus *(type non localisé) et* H. bimarginatus, *un néotype a été désigné pour* H. bimarginatus *dans la collection LeConte. Une clé d'identification de tous les taxons est présentée, ainsi qu'un diagnostic et une description des caractères morphologiques des adultes, la répartition géographique et l'habitat de chaque taxon. La position taxonomique d'*Hydaticus riehli *Wehncke, 1876 (region typique: Cuba) est consideree comme incertaine.*

Une analyse phylogénétique des genres et sous-genres d'Hydaticini indique que cette tribu comprend deux genres, Hydaticus *et* Prodaticus *Sharp, et qu'*Hydaticus *inclut les sous-genres* Hydaticus (s. str.), Guignotites *Brinck,* Hydaticinus *Guignot et* Pleurodytes *Régimbart, statut nouveau. L'arbre phylogénétique des Hydaticini et des espèces d'*Hydaticus s. str. *néarctiques est utilisé en combinaison avec d'autres caractéristiques de ces taxons pour édifier une hypothèse expliquant leur différentiation et leur répartition géographique. L'hypothèse est la suivante: le groupe ancestral d'Hydaticini este d'origine gondwandienne, et l'Afrique actuelle a été un centre évolutif ou des "vagues" successives de taxons ont originé. La faune nearctique d'*Hydaticus *est composée de trois "vagues" distinctes de colonisation de l'Amérique du Nord: une qui entra par la connection Nord-Atlantique (ancêtres de la ligneé* H. piceus-H. cinctipennis*), une qui arriva par l'Amérique centrale après la fermeture de l'isthme de Panama (ancêtre de la lignée* H. bimarginatus-rimosus*), et une qui pénétra par la connection béringienne* (H. modestus). *Ultérieurement, la vicariance des deux groupes ancestraux produisit le patron de répartition actuel.*

TABLE OF CONTENTS

INTRODUCTION

The genus *Hydaticus* Leach, 1817, as it is now known, occurs on all continents of the world except Antarctica. Zimmermann (1920) recorded 104 species in his world catalogue, only four of which were recorded from North America. Later authors (Leng, 1920; Blackwelder, 1939; Blackwelder and Blackwelder, 1948) concerned with North American taxa, modified the list and increased the total to five taxa. The only comprehensive treatments of adults of the world fauna of *Hydaticus* are those of Aubé (1838) and Sharp (1882). The last treatment of *Hydaticus* in North America, by Crotch (1873), consisted of a literature review and summation. Regional works treating various taxa of *Hydaticus* were for the Pacific Northwest (Hatch, 1953), California (Leech and Chandler, 1956), Baja California (Leech, 1948), Alberta (Larson, 1975), Utah (Anderson, 1962), North Dakota (Gordon and Post, 1965), Indiana (Blatchley, 1910), Florida (Leng and Mutchler, 1918; Blatchley, 1919; Young, 1954), Maine (Malcolm, 1971), Virginia (Matta and Michael, 1977), parts of the West Indies (Chevrolat, 1963; Young, 1953), and Canada (Wickham, 1895; Beaulne, 1917). Original descriptions, check lists, nomenclatural notes, and natural history notes comprise most of the remaining literature on North American taxa of *Hydaticus*.

Although only a few taxa of this genus are involved, there has been some confusion concerning their proper identities and limits (Wallis, 1939; Leech, 1948; Young, 1954; Larson, 1975). During this work adult specimens of the genus *Hydaticus* were examined in an attempt to understand specific limits, variation, and distribution. A phylogeny is reconstructed for the genera of the tribe Hydaticini, for the subgenera of *Hydaticus* and for the species groups which possess Nearctic representatives.

MATERIALS AND METHODS

Specimens of *Hydaticus* used in this study were borrowed from a number of institutions and private collections in North America and Europe. In addition, field collecting of specimens was carried out by the senior author in Ontario in 1975 and 1976; in 1978 specimens were examined during an extensive trip to various entomological museums in the U.S.A. and Canada. Some 2014 adult specimens of North American *Hydaticus* were examined. The collections from which material was borrowed and curators of these collections are listed below in association with abbreviations used in the text.

BMNH	British Museum (Natural History, London, England; M.E. Bacchus;
BMUW	University of Washington, Burke Museum, Seattle, Washington 98195; S.A. Rohwer;
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii 96818; G.A. Samuelson;
CASC	California Academy of Sciences, San Francisco, California 94118; D.H. Kavanaugh;
CISC	University of California, Berkeley, California 94720; J.A. Chemsak;
CMNH	Field Museum of Natural History, Chicago, Illinois 60605; E.M. Smith;
CNIC	Canadian National Collection, Agriculture Canada, Ottawa, Ontario, K1A 0C6; A. Smetana;
CUIC	Cornell University, Ithaca, New York 14853; L.L. Pechuman;
DBUM	University of Montreal, Montreal, Quebec, H3C 3J7; M. Coulloudon;
DEFW	University of Minnesota, St. Paul, Minnesota 55101; P.J. Clausen;
ELSC	California State College, Long Beach, California 90804; E.M. Fisher;
EMUS	Utah State University, Logan, Utah 84322; W.J. Hanson;
FNYC	F.N. Young, Indiana University, Bloomington, Indiana 47401; and University of Michigan, Museum of Zoology, Ann Arbor, Michigan 48109; I.J. Cantrall;
GWWC	G.W. Wolfe, University of Tennessee, Knoxville, Tennessee 37916;
ICCM	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania 15213; G.E. Wallace;

INHS	Illinois State Natural History Survey, Urbana, Illinois 61801; D.W. Webb, including W.U. Brigham collection;
ISUI	Iowa State University, Ames, Iowa 50010; R.E. Lewis;
JCAC	J.C. Aube, 283 des Franciscains, Quebec, Quebec;
JFBC	J.F. Brimley (now part of CNIC);
JFMC	J.F. Matta, Old Dominion University, Norfolk, Virginia 23508;
KSUC	Kansas State University, Manhattan, Kansas 66502; H.D. Blocker;
LACM	Los Angeles County Museum of Natural History, Los Angeles, California 90007; C.L. Hogue;
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138; J.C. Scott and M. Thayer;
MNHP	Museum of Natural History, Prague, Czechoslovakia; J. Jelinek;
MSUC	Michigan State University, East Lansing, Michigan 48824; R.L. Fisher;
MZHF	Museum of Zoology, University of Helsinki, Helsinki, Finland; H. Silfverburg;
NMDC	N.M. Downie, 505 Lingle Terrace, Lafayette, Indiana 47901;
NMSU	New Mexico State University, Las Cruces, New Mexico 88001; J.R. Zimmerman;
OSUC	Ohio State University, Columbus, Ohio 43210; C.A. Triplehorn;
OSUO	Oregon State University, Corvallis, Oregon 97331; J. Lattin;
PMNH	Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520; C.L. Remington;
ROMC	Royal Ontario Museum, Toronto, Ontario, M5S 2C6; G.B. Wiggins;
SCSC	St. Cloud State University, St. Cloud, Minnesota 56301; R.D. Gunderson;
SDSU	South Dakota State University, Brookings, South Dakota 57006; E.U. Balsbaugh;
SEMC	Snow Museum, University of Kansas, Lawrence, Kansas 66045; G.W. Byers;
SPMC	Provincial Museum of Natural History, Wascana Park, Regina, Saskatchewan, S4P 3V7; R.R. Hooper;
TAMU	Texas A & M University, College Station, Texas 77843; H.R. Burke;
UADE	University of Arkansas, Fayetteville, Arkansas 72701; E.P. Rouse;
UASM	University of Alberta, Strickland Museum, Edmonton, Alberta, T6G 2E3; G.E. Ball;
UBCZ	University of British Columbia, Spencer Museum, Vancouver, British Columbia, V6T 1W5; G.G.E. Scudder;
UCDC	University of California, Davis, California 95616; R.O. Schuster;
UCSE	University of Connecticut, Storrs, Connecticut 06268; R.E. Dubos;
UDCC	University of Delaware, Newark, Delaware 19711; P.P. Burbutis;
UGIC	University of Guelph, Guelph, Ontario, N1G 2W1; D.H. Pengelly;
UICU	University of Illinois, Urbana, Illinois 61801; J. Sternberg;
UMDE	University of Maine, Orono, Maine 04473; E.A. Osgood, Jr.;
UMRM	University of Missouri, c/o S.O. Swadener, INHS;
UCRC	University of California, Riverside, California 92502; S.I. Frommer;
USNM	United States National Museum, Washington, D.C. 20560; P.J. Spangler;
UVCC	University of Vermont, Burlington, Vermont 05401; R.T. Bell;
UWOC	University of Western Ontario, London, Ontario, N6A 3K7; W.W. Judd;
WEHC	W.E. Hilsenhoff, University of Wisconsin, Madison, Wisconsin 53706.

Standardized techniques were used in the dissection of the copulatory apparatus of adult males. The technique used for preparation of the aedoeagus was that of Smetana (1971, pp. 10-11).

Illustrations of male copulatory apparatus were drawn to scale using a Bausch and Lomb microprojector. Figures of the dorsal view of the left half of the body, and hind leg were drawn using a Leitz Wetzlar binocular, stereoscopic microscope equipped with a 20 x 20 square, ocular reticule. All illustrations are oriented with the anterior end of the specimen toward the top of the figure. Scanning electron micrographs of various body parts were taken with an "ETEC autoscan" after plating the structures with gold.

Measurements of body proportions were taken using a stereoscopic microscope fitted with an ocular reticule. Measurements were taken only when both end points of the structure were contained within the grid and were in sharp focus. Only mature specimens, in which elytra were joined completely along the suture and in which the head was drawn tightly into the pronotum, were used for measurements. The largest and smallest specimens of each species were chosen for the range of measurements. Measurements were made in terms of whole or parts of squares of the reticule and converted to millimeters. In addition, length of the median lobe was taken for adult males of each species.

Samples from various localities were selected for measurement on the basis of available material. In general, 10 males and 10 females were measured for each locality; however, for two species this was not possible, and most of the appropriate specimens were measured. Two measurements were made on each specimen of the sample; *viz.* total length of body (TL) and greatest width of body (GW).

A detailed description of the genus lists characteristics common to all species considered in this study. The following information is provided for each species treated: citation of the original description and references to other published taxonomic treatments, discussion of type material, summation of diagnostic characteristics, short descriptions of adults that accentuate the distinction among various species, notes on variation, notes about natural history based on either published records or field observations, distribution, chorological relationships, phylogenetic relationships, and material examined.

All locality records and the general Nearctic distribution given for each species were based on specimens examined. Some literature records could be based on misidentifications but they have been recorded for those areas outside the geographic limits of this study. In the locality lists of specimens examined, the following information is provided: Country, State or Province, County or Regional Municipality or District, locality, date, collector, collector's remarks, acronym of the collection from which the specimens were received, and the number of specimens received from that collection. Data were recorded as they appeared on the label except that the first two digits of the year were deleted and the months were converted to Roman numberals (i.e., 21 May, 1967 became 21.v.67). In a series of specimens from a single locality, the label with the most complete data for that locality was the one recorded. Complete locality records for such common species as *H. modestus*, *H. piceus* , and *H. bimarginatus* are omitted. Copies of these records are stored at the Department of Environmental Biology, University of Guelph and at the Strickland Museum, University of Alberta. Persons desiring copies of these lists should contact the authors or these Departments.

The greatest problem facing any taxonomist is determining the best manner in which to recognize a biological species from series of museum specimens. Various techniques are used for inferring species status by means of clues supplied by the museum specimens. Our procedure involved grouping specimens by similarity of the male aedoeagus, especially the median lobe. The underlying assumption is that dissimilar median lobes of various phena, especially if correlated with consistent differences in other characters, represent reproductive isolating mechanisms necessary for fulfilment of the biological species definition (Mayr, 1963, pp. 91, 663) (for a more detailed discussion, especially of exceptions, see Erwin, 1970; Noonan, 1973; Whitehead, 1972). The next step involved associating females with males of that same taxon.

Each species of *Hydaticus* of North America is sympatric with at least one other species in some part of its range. This area of sympatry was considered a test of species status versus subspecific status (Mayr, 1969; Ross, 1974). If no intermediate specimens were observed, species status was considered to be confirmed. The areas of sympatry are indicated under the treatment of each taxon in the section on chorological relationships.

In practice, identification of North American specimens of *Hydaticus* is not difficult once the specific limits of variation are understood. Each taxon has distinctive features which should allow ready assignment of specimens.

The subgenera of *Hydaticus* proposed by Guignot (1950) are used herein because they are monophyletic and represent natural evolutionary units. There is the probability of increased information from such a taxonomic division, and subgeneric characters are used within the key to species. The characters separating two subgenera were recently clarified, expanded, and strengthened by Franciscolo (1968).

NATURAL HISTORY

Very little is known about natural history of North American species of *Hydaticus*, but European authors have contributed more to the knowledge of natural history of this genus. Galewski (1971), in his work on Dytiscidae of Poland, recorded the preference of *Hydaticus* for ditches, pools, and ponds with abundant vegetation, a deep layer of plant debris or detritus and low acid content. Adults frequent temporary pools in early spring to take advantage of available food, expecially the larvae of snow-melt mosquito populations, but they spend the summer in more permanent waters. The breeding season of the European species is from late spring to early summer, mainly in May and June. This breeding season often coincides with development of preferred oviposition sites, which are aquatic, vascular plants, belonging to genera such as *Alisma*, *Iris*, and *Typha*.

Adult females of *Hydaticus* possess genital valves which are long, narrow, and knife-like, but without serrations (Böving 1912; Galewski (1971)). This piercing type of ovipositor is well adapted for endophytic, egg deposition (Balduf, 1935).

Larvae of *Hydaticus* are good swimmers, when compared to most other larvae of Dytiscidae, because of the dense fringe of swimming hairs on all legs and on the last two abdominal segments. The three larval stages are passed within the littoral zone of the breeding areas, although some individuals venture into open water. The large tracheae of larvae are filled with air; consequently larvae float to the surface when not swimming. Vegetation is used as resting and feeding sites, but the larvae are awkward when crawling. The prey of larvae are small naiads of Odonata and Ephemeroptera, and larvae of Trichoptera and Diptera (Galewski, 1971). Pupation occurs on land near the larval habitat in the typical dytiscid manner. In England, Balfour-Browne (1950) recorded emergence of adults from pupae during August and September. Many newly emerged adults invade temporary pools in late summer and autumn (Galewski, 1971). Adults overwinter under leaf litter and moss on land, often a considerable distance from the nearest body of water (Galewski, 1964, 1971).

There are few known natural enemies of *Hydaticus*. The gregarine, *Bothriopsis histrio* was recorded from individuals by Balduf (1935). Pujatti (1953) recorded the metacercariae of the trematode genus *Lecithodendrium*. The chalcidoid *Mesotocharis syclospila* Forst. (Hymenoptera: Eulophidae) parasitized eggs of *Hydaticus* within the stems of *Alisma* when that part of the plant was above water (Balduf, 1935).

TAXONOMIC CHARACTERS AND TERMS

Sexual dimorphism. – Adults of *Hydaticus* possess five main characters which are sexually dimorphic, other than those of the male and female genitalia. 1) In the North American taxa studied, female specimens are, on average, shorter and narrower and have a general outline which is more symmetrically oval than that of males. 2) Male specimens are smooth except for two rows of widely spaced, shallow punctures on each elytron. Most females have sculpturing on the prothorax and/or elytra. The sculpturing or rugosity varies from shallow, widely spaced, longitudinal depressions to deep, closely spaced, irregular folds or furrows. Rugosity varies markedly within and among populations; general trends are noted under each species description and discussion. 3) Protarsal claws of males are longer and are bent more sharply at the base than are their female counterparts. Mesotarsal claws are of different lengths and differ in amount of curvature between male and female specimens. Unlike other genera of Dytiscidae, claws of males differ only slightly among taxa. 4) The three basal tarsomeres of the forelegs of males are expanded into circular acetabula (Fig. 2), and posses sucker-like setae which adhere to the pronotum of the female during copulation. Four large suckers are located on the basal segment and these are supplemented by 16 to 18 smaller suckers. 5) The three basal mesotarsomeres of adult males are expanded into elongate, oval acetabula. Mesotarsal suckers are of about equal size *inter se*. Eight suckers are on the anterior side of the tarsal midline and seven on the posterior side (Fig. 3). The number of suckers on each acetabulum is variable and is difficult to ascertain on many specimens as the suckers are easily broken. Students of Dytiscidae (Wickham, 1893; Chatanay, 1910; Balfour-Browne, 1940, 1950; Larson and Pritchard, 1974) have studied adaptations within the family. Their works indicated that the form of the front tarsi of adult males and the arrangement and number of sucker-like setae were diagnostic for higher taxa. Within the North American males of *Hydaticus* this character was uniform yet varied. The same basic arrangement is found throughout; however, arrangement and number of modified setae varied between legs of an individual and within and among species. These were without diagnostic value in the taxa studied; however, trends in the number of suckers and their size and pattern are used as a phylogenetic character.

Head. – In Nearctic *Hydaticus*, colour pattern and the presence or absence of large spots or maculae on the frons is an important diagnostic character. The frons varied in colour from a black band against a yellow ground colour to reddish-brown throughout, with infuscated areas.

Pronotum. – Colour of pronotum varied from yellow to black. In most species there is a basal, black band of variable width. This band is useful in recognition of some specimens of *H. rimosus* because it extends to the anterior margin in the form of a wide band. *H. piceus* and *H. cinctipennis* specimens have a more or less unicolourous pronotum except for discal infuscations. Curvature of the posterior margin of the pronotum is useful for separation of subgenera. In adults of subgenus *Guignotites*, the posterior margin is sinuate. The portion along the midline is extended posteriorly, and the portions lateral to the midline are shortened, but the postero-lateral corners are recurved into an acute angle (Figs. 37, 43, 48, 49). In adults of the subgenus *Hydaticus*, the portions lateral to the midline are not as conspicuously shortened in length and the postero-lateral corners of the pronotum are truncate (Figs. 7, 8, 9, 22, 30).

Metatarsal claws. – Shape of the claws of the hind legs is an aid in distinguishing between some males of the two species of the subgenus *Guignotites*. In *H. bimarginatus*, the anterior (shorter, inferior) claw is deflected downward at the apex (Fig. 44), whereas in *H. rimosus* it is not (Fig. 55). This character was considered unreliable because of the possible effect of abrasion on shape of the apex of the claws. Some males of *H. bimarginatus* lacked the apical deflections. The relative length and shape of the metatarsal claws are given in the description of each taxon.

Metatibial chaetotaxy. – Balfour-Browne (1950) emphasized the use of arrangement, number, and size of spines on the legs for separating the higher taxa of Dytiscidae. Guignot (1950) and Franciscolo (1968) used chaetotaxy of metatibiae for separating the subgenera of *Hydaticus*. In North American specimens, the row of spines on the posterior (upper, nearest the venter) side of the metatibia is either in a straight line and parallel to the outer margin of the tibia (subgenus *Hydaticus*, Figs. 10, 23, 31); or the row is curved inward basally, and thus does not form a parallel line with the outer margin (subgenus *Guignotites*, Figs. 38, 50). Within the subgenus *Guignotites*, the number of large spines on the anterior (lower) side of the metatibiae is important in separating the two species. These spines were broken off in some individuals and if so, the large pits where the spines originated were counted. The most reliable way to determine number of spines per tibia is to average the number of spines on both metatibiae of the same specimen. The number of spines varies between specimens and between metatibiae of the same specimen, but the specific limits do not overlap and they are in accord with other taxonomic characters. In *H. bimarginatus* there are a number of smaller spines basally which were not counted. Under each species in which the lower, metatibial spines were used for diagnosis, a table is provided of the average number of spines per metatibia from the specimens used for the descriptive measurements.

Metasternum. – The metasternum of dytiscid adults is displaced by the anterior extension of the hind coxae, resulting in the formation of a relatively narrow, transverse sclerite which is indented on each side of the median portion. The area lateral to the median indentation is termed the "metasternal wing" (Balfour-Browne, 1950). The straight anterior margin of the metasternal wing is a diagnostic characteristic of members of the genus *Hydaticus*.

Dorsal colour pattern. – Franciscolo (1968) suggested that colour patterns in the subgenus *Guignotites* were useful in the recognition of some of the species only. The dorsal colour pattern, however, is useful in the identification of North American material due, in part, to the small number of taxa concerned. Specimens of *H. piceus* and *H. cinctipennis* are yellowish to reddish-brown, whereas those of the other taxa are black. Adults of all taxa have the general colour disrupted by various amounts of yellow which varies from an indistinct lateral border in *H. piceus*, to lateral and/or sub-lateral stripes among other taxa, to a highly developed pattern in some females of *H. modestus* (Fig. 9).

Male genitalic appendages. – The terms used for the genitalic sclerites were those of Edwards (1950), except for the specialized structures of *Hydaticus*, as discussed by Guignot (1933) whose terms were retained.

The male genital capsule,*in situ,* is rotated 90° to the left(*i.e.*, left paramere is next to sternum 7). This sinistral twist of the genitalic armature is common to all Adephaga, except Gyrinidae (Edwards, 1950; Balfour-Browne, 1950). Components of the genitalic capsule are illustrated in Figs. 4 and 5, and consist of: 1) sternum 8 which is joined to a semi-circular anterior arch; 2) the basal portion of sternum 9, pleuron 9, and tergum 9 which are fused into a dorso-ventral circular ring surrounding the more posterior structures in repose; 3) an elongate rod or spicule lying on the membrane between the parameres which is possibly a posterior section of sternum 9 separated from an anterior portion; 4) the preputial covering which is strengthened but not sclerotized at the apical portion of a membrane which joins the parameres ventrally; 5) the epipenite, on the dorsal side of the preputial covering, next to the median lobe; 6) symmetrical, hairless parameres which are parallel and of equal length; 7) the median lobe which extends slightly beyond the parameres and articulates with them basally. All of these structures are joined by an ensheathing membrane, except for the dorsal side of the parameres and the median lobe. The aedoeagus is composed of median lobe, parameres, and epipenite.

The position and form of epipenite are important for subgeneric diagnoses. Males of the subgenus *Hydaticus* have the epipenite on the preputial covering (*i.e.*, on the opposite side of the preputial covering to the median lobe, Figs. 4 and 5). In males of the subgenus *Guignotites* the epipenite is internal, on the preputial covering, next to the median lobe. The transition from external to internal position of the epipenite on the preputial covering reverses the orientation of the median and lateral arms of the epipenite (Figs. 4 and 41). The epipenite in males of the subgenus *Guignotites* is generally not as heavily sclerotized as that of males of subgenus *Hydaticus*. In the subgenus *Hydaticinus*, represented only by the South American *H. rectus*, the epipenite is still less sclerotized and is inserted into the apex of the preputial covering.

The shape of the epipenite and of the apex of the median lobe are important in species diagnosis. The epipenite is a trilobed structure consisting of a median arm and a pair of lateral arms. Length of the lateral arms, when compared to length of the median arm, and shape of the three arms are important in specific assignment. In side view, the apex of the median lobe varies from truncate to acutely angled. The median lobe possesses lateral flanges (Figs. 4 and 5) of a tough membranous substance. The degree of posterior extension of these flanges in relation to the apex of the median lobe is a useful character.

CLASSIFICATION

Genus Hydaticus Leach

Hydaticus Leach, 1817: 69, 72 [*nec Hydaticus* Schoenherr, 1825 (Coleoptera: Curculionidae)]. Nearctic references only - Aubé, 1838: 155 (*ex parte*). - Crotch, 1873: 403. - Sharp, 1882: 907, 908. - LeConte and Horn, 1883: 67. - Horn, 1883: 380. - Wickham, 1895: 149. - Blatchley, 1910; 232. - Beauline, 1917: 124. - Blatchley, 1919: 314. - Leech, 1948: 419. - Young, 1953: 6. - Hatch, 1953: 235. - Young, 1954: 113. - Leech and Chandler, 1956: 332. - Anderson, 1963; 56. - Gordon and Post, 1965: 23. - Malcolm, 1972: 30. - Larson, 1975: 405. - Matta and Michael, 1977: 48.

Type-specimens. – *Dytiscus transversalis* Pontoppidian, 1763; designated by Curtis, 1825: 95 (attributing the species to Fabricius), and by Crotch, 1873: 403. Hope, 1939: 131 cited *Dytiscus hybneri* Fabricius, 1787(=*Dytiscus seminiger* Degeer, 1774) as generitype Duponchel, 1845 (6): 728 designated *Dytiscus fasciatus* Fabricius, 1775 [=*Sandracottus fasciatus* (Fabricius, 1775)] as generitype but this species was not listed by Leach, 1817 (from Leech, 1948: 419).

Diagnostic combination. – Dytiscinae with the following combination of characters: outer margin of metasternal wings straight; outer (shorter) spurs at apex of metatibiae acute; apex of prosternal process rounded; and posterior margins of four basal tarsomeres of hind legs with dense fringe of flat, golden hairs.

Description. – *Adults.* Size medium (North American specimens, TL from 10.9 to 15.4 mm, GW from 5.9 to 8.0), body form ovate (ratio GW:TL 0.47 to 0.58), outline continuous, widest just behind middle. Colour various, from yellowish-brown to black; surface shining or dulled by rugosity.

Microsculpture singular, isodiametric, very fine (difficult to see except at high magnification), small pores scattered throughout. Sculpture of elytron consisting of two linear rows of shallow punctures, not apparent on some females because of deep, irregular wrinkles on elytron and/or pronotum.

Head. – Form as in subfamily, except inner anterior margin of eyes slightly emarginate, but not as in Colymbetinae (Balfour-Browne, 1950). Labrum excised at middle, yellowish to reddish-brown, with brush of fine, short hairs. Clypeus indistinct, fused with frons, yellowish to reddish-brown. Frons of most specimens darkened basally, reddish-brown to black, many specimens with yellowish maculae (Figs. 6,47). Occiput short, reddish-brown to black. Palps and antennae yellowish to reddish-brown, segments often infuscated apically. Structure of mouthparts not examined for specific or subgeneric differences.

Thorax. – Pronotum with lateral margins acute but not margined; wider at base than at head, with lateral outline rounded; antero-lateral margins produced anteriorly as acute projections; base continuous with bases of elytra, posterior margin more or less sinuate, projected posteriorly opposite scutellum, curved forward lateral to scutellum. Scutellum visible, about 1.5 times as long as wide. Prosternal process with ventral surface convex basally to flat apically, apex broadly rounded, marginal bead complete except apically. Metasternum with short, deep notch for reception of prosternal process; metasternal wings with anterior margin straight, not extended to epipleura, posterior margin sinuate. Metacoxal plates as wide or wider than long (ratio from 1.0 to 0.77); metacoxal processes margined, rounded, separated by posterior incision; metacoxal lines convergent on metacoxal processes and divergent on metacoxal plates, effaced anteriorly.

Legs. – Foretarsi of males with tarsomeres 1, 2, and 3 expanded as a broad circular acetabulum (Fig. 1). Tarsomere 5 longest, others subequal in length. Four rows of sucker-like, circular, modified setae or cupules on acetabulum; ventral surface of tarsomere 1 with two rows of four and five suckers each, tarsomere 2 with one row of seven suckers, tarsomere 3 with one row of six suckers. Tarsomere 4 with brush of short, golden setae along antero-ventral margin, tarsomere 5 with two long parallel rows of similar setae ventrally. Anterior claws slightly longer and less robust than posterior claws. Male protibiae and profemora hollowed out ventrally for reception of acetabula of protarsi and protibiae respectively (Fig. 1). Antennal comb and marginal setae of protibiae numerous and longer than those of mesotibiae. Protibiae with pegs along posterior margin near apex, opposed to pits along dorsal surface of tarsomeres 1 and 2 (Fig. 1) (Larson and Pritchard, 1974). Mesotarsi of males with tarsomeres 1, 2, and 3 moderately expanded as an elongate oval acetabulum (Figs. 2 and 3); tarsomere 5 longest, and others subequal, tarsomere 4 of some specimens longer than 2 or 3. Ventral surface of tarsomere 1 with seven suckers, 2 and 3 with four suckers. Acetabulum with long lateral setae (Fig. 2). Mesotibiae and mesofemora not modified for reception of mesotarsi or mesotibiae, respectively. Tarsomere 4 with brush of short golden setae along antero-ventral margin, tarsomere 5 with two long parallel rows ventrally. Claws of middle legs longer than those of forelegs, more evenly arcuate, subequal in length, and of similar shape.

Protarsi of females not expanded; tarsomere 5 longest, others subequal. Protibiae and profemora not hollowed out ventrally. Claws subequal in length and similar in shape. Mesotarsi of female not expanded; tarsomere 5 longer than 1, 1 longer than remaining ones which are subequal. Mesotarsal claws longer than, or subequal to, protarsal claws. Otherwise, legs of females similar to those of males.

Elytra. – Continuous with outer margin of pronotum at base, widest just behind middle, apices rounded or sinuate (Fig. 18). Shining or dulled by rugosity baso-laterally (Fig. 17). Epipleuron extended to about middle of last visible (6th) abdominal segment. Lateral margins with irregular row of long, fine setae extending from basal third almost to apex. Rows of translucent, rectangular spots beginning marginally in basal third, curving inward posteriorly and in most specimens confluent with division between lateral and sub-lateral stripes if the latter are present. Colour yellowish-brown to black, many specimens with yellow marginal stripes, and/or sub-lateral stripes, latter recurved suturally at base in some taxa, but in adults of most taxa curved away from margin posteriorly. Some specimens with transverse, yellow fasciae sub-basally, with longitudinal vittae from fasciae ending sub-apically (Fig. 9).

Taxonomic placement. – Most authors placed *Hydaticus* in the tribe Hydaticini of the subfamily Dytiscinae, except Balfour-Browne (1950), who included it in the subtribe Hydaticina of the tribe Dytiscini. The only other genus in the tribe Hydaticini is the monobasic *Prodaticus* with *P. pictus* Sharp, 1882, known from Persia, Baluchistan, India and Arabia (Zimmermann, 1920). The dibasic *Pleurodytes* Regimbart with *P. dineutoides* (Sharp, 1882) known from Java and Borneo (Zimmermann, 1920; Vazirani, 1969) and *P. epipleuricus* (Régimbart, 1891) known from Tennasserim, Malewan (Vazirani, 1969) is also a member of Hydaticini. However, it does not deserve generic status and *Pleurodytes* is treated here as a subgenus (NEW STATUS) of *Hydaticus s. lat.* (see PHYLOGENY). The monobasic *Notaticus* with *N. fasciatus* as type species was described as belonging to the tribe Hydaticini.

Spangler (1973) placed *N. fasciatus* as a junior synonym of *Aubehydrus speciosissimus* Guignot 1942 and retained it within the subfamily Aubehydrinae. A key to the world genera of Hydaticini was presented by Zimmermann, 1919: 225, and by Zimmermann and Gschwendtner, 1937: 4.

KEY TO THE SPECIES OF *HYDATICUS* OF NORTH AMERICA

1 (0) Pronotum with postero-lateral corners sharply and distinctly acute (best seen in side view), posterior pronotal margin markedly sinuate and recurved laterally (Figs. 37, 43, 48, and 49); metatibia with row of spines on disc of posterior (upper) surface curving inward basally, not parallel to outer tibial margins (Figs. 38 and 50); and epipenite at apex of preputial covering. (Subgenus *Guignotites* Brinck) 4

1′ Pronotum with postero-lateral corners truncate, posterior pronotal margin moderately sinuate but not revurved laterally (Figs. 7, 8, 9, 22, and 30); metatibia with row of spines on disc of posterior surface straight, parallel to outer tibial margin (Figs. 10, 23, and 31). Epipenite anterior to apex of preputial covering (Figs. 4 and 5). (Subgenus *Hydaticus*). 2

2 (1′) Elytra with broad, lateral, yellow stripes, without sub-lateral stripes but some females vittate (Figs. 7, 8 and 9); colour black; frons black with two, narrow, transverse, yellow maculae (Fig. 6). Epipenite of aedoeagus W-shaped, lateral arms as long as or longer than median arm (Fig. 13); median lobe with lateral flanges extending almost to apex (Fig. 12)[1] .... *H. modestus* Sharp

2′ Elytra with broad, lateral, yellow stripes absent, narrow, indistinct, marginal area present or absent; colour reddish-brown; frons not black, without narrow, transverse, yellow maculae. Epipenite W-shaped, but length of lateral arms 0.66 or less than that of median arm 3

3 (2′) Elytra with sub-lateral, longitudinal, yellow stripes, with or without basal fasciae (Fig. 22); form elongate oval, more parallel sided. Epipenite of aedoeagus with lateral arms less than 0.50 length of median arm (Fig. 26); apex of median lobe acute in side view (Fig. 24) .... *H. cinctipennis* Aubé

3′ Elytron without sub-lateral, longitudinal stripes, yellow marginal area present or not, basal fasciae absent (Fig. 30); form oval, sides more arcuate. Epipenite of aedoeagus with lateral arms about 0.66 length of median arm (Fig. 34); apex of median lobe with projection in side view (Fig. 32) .... *H. piceus* LeConte

4 (1) Median lobe of aedoeagus angulate at apex in side view (Fig. 39). Anterior (lower) disc of metatibiae with an average[2] of more than 10 large spines ($\bar{x} = 11.8$; max. = 14; min. = 9) (Fig. 45); basal black band of pronotum restricted in most specimens to basal 0.33, extended in few specimens to anterior margin as broad band; elytron with sub-lateral stripes without inward extensions of yellow, transverse fasciae absent (Fig. 37) .... *H. bimarginatus* Say

4′ Median lobe of aedoeagus truncate at apex in side view (Fig. 51). Anterior disc of metatibiae with average of less than 10 large spines ($\bar{x} = 6.2$; max. = 10;

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[1] While this manuscript was in press, a paper by Nilsson (1981) appeared which suggests that the valid name of this taxon is *H. aruspex* Clark, 1864.

[2] one-half the total number of spines on both metatibiae.

min. = 2) (Fig. 56); basal black band of pronotum often extended to or almost to anterior margin; elytra with sub-lateral stripes, sometimes with inward extensions of yellow, transverse fasciae present in some specimens (Figs. 48, 49) .... *H. rimosus* Aubé

Subgenus Hydaticus

Guignot, 1950: 104. – Franciscolo, 1968: 48.

Diagnostic combination. – Frons black or infuscated basally, reddish-brown. Frons, when reddish-brown, lacking distinct, contrasting maculae; maculae represented by variable infuscations (Figs. 21 and 29). Frons, when black, with distinct, yellow maculae (Fig. 6). Pronotum with posterolateral corners truncate, pronotal margin moderately sinuate posteriorally but not recurved laterally (Figs. 7, 8, 9, 22 and 30). Row of spines on disc of posterior surface of metatibiae straight (Figs. 10 and 23) or only slightly curved inward basally (Fig. 31). Elytra black to yellowish-brown; stripes absent, or only marginal, or only sub-lateral present; transverse basal fascia present or absent. Elytra, when black, with yellow colouration in form of transverse basal fasciae, and longitudinal vittae in some female specimens (Fig. 9). Epipenite of male genitalic capsule on opposite side of preputial covering to the median lobe (Figs. 4 and 5); heavily sclerotized.

Hydaticus (Hydaticus) modestus Sharp[3]

Figs. 4-19. Distribution map, Fig. 20

Hydaticus modestus Sharp, 1882: 650. -- Wallis, 1939: 126, 127. -- Hatch, 1953: 235. -- Leech and Chandler, 1956: 332. -- Anderson, 1962: 73. -- Gordon and Post, 1965: -- Larson, 1975: 405.

Hydaticus americanus Sharp, 1882: 651. -- Zimmermann, 1919: 225. --Wallis, 1939: 126, 127.

Hydaticus stagnalis, Crotch, 1873: 404. -- Horn, 1883: 280. -- Wickham 1895: 150. -- Blatchley 1910: 232, 233. -- Beaulne, 1917: 124. -- Zimmermann, 1919: 225, 226 (*ex parte*). -- Zimmermann and Gschwendtner, 1937: 10 (*ex parte*). -- F. Balfour-Browne, 1950: 300 (*ex parte*). -- Zaitzev, 1953: 307 (*ex parte*). -- Watts, 1970: 727. -- *nec* Fabricius, 1787: 191.

Hydaticus laevipennis, Sharp, 1882: 651. -- Blatchley, 1910: 233. -- Beaulne, 1917: 124. -- *nec* Thomson, 1867: 88.

Hydaticus rugosus Poppius, 1905: 23, 24. NEW SYNONOMY. Zaitzev, 1910: 44. -- Zimmermann and Gschwendtner, 1937: 17. -- Zaitzev, 1953: 330.

Hydaticus bimarginatus, Wickham, 1895: 150. --*nec* Say, 1931: 5.

Notes on synonomy and type material. – Holotypes of *H. modestus* and *H. americanus* were examined by Larson (1975) and were not re-examined in this study. The holotype (♀) of *H. rugosus* was borrowed from the Zoological Museum, University of Helsinki, Helsinki, Finland. It is labelled as follows: Ust Aldan; Fl. Lena; B. Poppius: 877 (pink label); Mus. Zool. H:fors, Spec. type No. 1953, *Hydaticus rugosus* Popp.

Nomenclature of Nearctic *H. modestus* and Palaearctic *H. stagnalis* (Fabricius, 1787) has long been confused. J. Balfour-Browne (1944, p. 355) proposed *H. continentalis* as a new name for *H. stagnalis* which was described originally as a member of *Dytiscus* and thus the latter name is itself a junior homonym of *Dysticus stagnalis* Fourcr., 1785, which is itself a junior synonym of *Dytiscus semisulcatus* O. Müller, 1776. Most subsequent European workers -- *e.g.*, F. Balfour-Browne (1950) and Guignot (1947), did not accept the name *H. continentalis*,

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[3] While this manuscript was in press, a paper by Nilsson (1981) appeared which suggests that the valid name of this taxon is *H. aruspex* Clark, 1864.

Table 1. Variation in the length and greatest width of body of selected samples of North American taxa of *Hydaticus* (Coleoptera: Dytiscidae). Measurements in mm.

				Total Length		*Greatest Width*	
Taxon	Locality	Sex	N	Mean	Range	Mean	Range
H.modestus	Creston, B.C.	♂	10	14.2	13.7-15.4	7.6	7.2-8.0
		♀	10	13.6	12.8-14.2	7.3	7.1-7.7
	Edmonton,Alta.	♂	10	14.7	13.8-15.2	7.6	7.0-8.0
		♀	10	14.4	13.7-15.1	7.4	7.1-7.6
	Massachusetts	♂	10	14.0	13.3-14.5	7.3	6.9-7.5
		♀	10	13.7	13.0-14.7	7.2	6.8-7.6
H. piceus	Illinois	♂	10	12.6	12.0-13.1	7.0	6.7-7.2
		♀	10	12.6	11.7-13.3	6.9	6.6-7.2
	Ontario	♂	10	13.5	13.1-14.0	7.6	7.2-7.9
		♀	10	12.9	11.6-13.7	7.3	6.6-7.6
	Massachusetts	♂	10	13.5	12.6-14.0	7.4	6.9-7.8
		♀	10	13.0	11.7-13.7	7.2	6.8-7.6
H.cinctipennis	Northern specimens (Conn., Del., Mass., N.J., R.I., Va.)	♂	12	13.7	13.1-14.7	7.3	6.9-7.6

(continued on next page)

Table 1 (continued)

Taxon	Locality	Sex	N	*Total Length* Mean	Range	*Greatest Width* Mean	Range
		♀	11	13.8	13.3-14.2	7.4	7.1-7.6
	Southern specimens (Fla., Ga.)	♂ 1 12.8 7.3		-			
		-					
		♀	1	12.7	-	6.9	-
H.bimarginatus	Dismal Swamp, Va.	♂	10	12.1	11.6-12.4	6.5	6.3-6.6
		♀	10	11.9	10.9-12.6	6.3	5.8-6.7
	Highlands Co.,Fla.	♂	10	12.0	11.4-12.6	6.4	5.9-6.8
		♀	10	12.0	11.2-12.6	6.5	6.0-6.9
	Texas	♂	10	12.5	11.7-13.1	6.7	6.4-7.0
		♀	10	12.4	11.6-13.1	6.7	6.3-7.1
H.rimosus	Cuba;Bahamas,B.W.I.	♂	9	11.9	11.2-12.3	6.3	6.2-6.7
		♀	6	12.3	11.9-12.6	6.6	6.4-6.9

(continued on next page)

Table 1 (continued)

Taxon	Locality	Sex	N	*Total Length* Mean	Range	*Greatest Width* Mean	Range
	Mexico; Guatemala: (Br. Honduras;) Honduras	♂	15	12.4	11.9-12.7	6.7	6.3-7.0
		♀	12	13.0	12.3-13.7	6.7	6.4-7.0

Table 2. The numbers of *Hydaticus (H.) modestus Sharp with the development of yellow on the elytra, characterized as vittate (V), fasciate (F), and non-fasciate (N); and of elytral sculpture, characterized as rugose (R), and smooth (S).*

	Development of Yellow on Elytra							*Sculpture of Elytra*		
Females	*Females*				*Males*					
Locality	V	F	N	Total	F	N	Total	R	S	Total
British Columbia,Oregon, California, Washington	31	2	9	42	19	3	32	2	40	42
Alaska, Alberta, North West Territories	60	31	21	112	34	61	95	109	3	112
Montana, Wyoming, Utah	0	2	4	6	0	1	1	4	2	6
Manitoba, Saskatchewan	31	4	4	39	29	5	34	33	6	39
Michigan, Minnesota, Wisconsin	41	12	4	57	33	8	41	12	45	57
Illinois, Indiana, Iowa, Missouri, Ohio	20	12	1	33	14	8	22	5	28	33
Ontario, Quebec	46	16	13	75	38	20	58	5	70	75
New England states, New York, Pennsylvania	43	18	12	73	28	25	53	0	73	73

presumably because the North American *H. modestus* was, in their opinions, incompletely studied (see F. Balfour-Browne, 1950, pp. 299-300; and Guignot, 1947, p. 228, footnote #2) even though Wallis (1939) had presented evidence that the two were separate. The distinguishing features used by Wallis were that *H. modestus* is narrower and more parallel-sided than *H. stagnalis* and males of *H. modestus* are not vittate as are males of *H. stagnalis*. The anterior metatarsal claw of *H. modestus* is proportionately shorter and weaker than the posterior claw when compared to that of *H. stagnalis*. The elytral apices are sinuate in females of *H. modestus* (Figs. 9 and 18). All of these differences were confirmed in this study and, in addition, the aedoeagus of males differed consistently. The epipenite of *H. continentalis* (Fig. 15) has the middle arm much more expanded apically, and the lateral arms are shorter in relation to the median arm, when compared to *H. modestus* (Fig. 13). The median lobe of male *H. continentalis* (Fig. 16) is more rounded basally and is much longer ($\bar{x} = 2.9$ mm, N = 5) than that of *H. modestus* males ($\bar{x} = 2.7$ mm, N = 12). Thus, the correct name for the Palaearctic form is *H. continentalis*.

Specimens of *H. modestus* run consistently to *H. rugosus* Poppius 1905 and not to *H. continentalis* (= *H. stagnalis*) in Zaitzev's key (1953). The type of *H. rugosus* was examined and found to be within the range of variation of similar rugose specimens of *H. modestus* from Alaska, Alberta, and the North West Territories. Thus, *H. rugosus* is considered to be conspecific with *H. modestus*. This synonomy supports the distinctness of *H. modestus* from *H. continentalis*, because *H. rugosus* was described by Poppius who had an adequate knowledge of *H. continentalis*. The type of *H. rugosus* is from Ust Aldan which is in Yakutskaya region of the Central Siberian Uplands of the U.S.S.R. This specimen is illustrated in Figure 9.

Wallis (1939) doubted the validity of *H. cinctipennis* Aubé 1838 and suggested that it was possibly conspecific with *H. modestus*. However, he believed that there was insufficient evidence for placing the names in synonomy. It would appear that Wallis had not seen Aubé's rather detailed original description of *H. cinctipennis* as he cited only Sharp's (1882) subsequent description and the taxonomic notes of Zimmermann (1919). In the present study, *H. cinctipennis* is considered as a valid and distinct taxon, separate from *H. modestus*.

Blatchley (1910), as noted by Larson (1975), seemed to have assigned vittate females to *H. stagnalis* and the males and non-vittate females to *H. laevipennis*. Larson (1975), who examined the types of *H. modestus* and *H. americanus*, stated that the latter is a lightly sculptured female of *H. modestus* which is the valid name because of page priority.

Diagnostic combination. – Adults are recognized by the narrow, transverse, yellow maculae on the frons (Fig. 4). They are the only North American members of the subgenus *Hydaticus* with a black ground colour, lateral stripes, and vittate females (Fig. 9). Median lobe and epipenite of aedoeagus are distinctive.

Description. – Length from 12.8 to 15.4 mm, width from 6.8 to 8.0 mm, other measurements in Table 1. Form ovate, moderately convex. General colour black. Head black, except for clypeus and two narrow, yellowish to reddish-brown, transverse maculae on frons (Fig. 6). Pronotum yellowish to reddish-brown except for narrow, transverse, black band at base, band not extending to lateral margins and restricted to basal third (Fig. 7). Elytra piceous to black; lateral yellow stripes distinct, slightly recurved suturally at base, marginal, ending before elytral apex except in very few specimens, appearing divided medially because of rows of translucent rectangles (Fig. 7). Elytra, except for lateral stripes, piceous to black (Fig. 7), or with transverse, basal fasciae (Fig. 8), or some adult females with fasciae and two to 10 longitudinal vittae (Fig. 9), fasciae and vittae yellow to reddish-yellow. Ventrally, prosternum yellow to reddish-yellow; remainder of thorax black; abdominal sterna black, margins of many specimens piceous and with yellow to piceous maculations laterally. Profemora and mesofemora yellowish-red with infuscations, tibiae more infuscated, tarsi darkest. Hind legs piceous to black. Rugosity absent or present, in the form of a few, shallow depressions baso-laterally on elytra or deep, irregular wrinkles on pronotum and most of elytra except area along suture (Figs. 9, 17). Anterior metatarsal claw, bent downward at tip, less than 0.50 length of posterior claw. Median lobe of aedoeagus moderately long ($\bar{x} = 2.7$ mm, N

= 12), truncate basally, apex notched in side view (Fig. 11). In ventral view, lateral flanges extending almost to tip, apex of median lobe not modified (Fig. 12). Epipenite with lateral arms equal or subequal in length to median arm, expanded medially, thickened and narrowed basally (Fig. 13). Parameres narrow, acute at apex, with narrow, translucent flange on apical third (Fig. 14).

Variation. – Adults of *H. modestus* vary in the amount of rugosity and yellow coloration on the elytra. Both of these characteristics show patterns of geographical variation. Data for selected samples of *H. modestus* are presented in Table 2 and shown schematically in Figure 19.

The pronotum and elytra of males are smooth. In females, however, rugosity varies from nil to almost all of pronotum and elytra being covered by deep, irregular wrinkles (Figs. 9, 17). Elytra of females from British Columbia, Washington, Oregon, and California are predominantly smooth, whereas those from Alaska and east of the Rocky Mountains to southeastern Manitoba are consistently rugose in sculpture. Specimens from scattered localities in northern Ontario and northern Quebec could indicate an eastward extension of this form. A few rugose females were seen in population samples from Wisconsin, Minnesota, and Michigan. Females from eastern Manitoba, eastern and mid-western U.S.A., southern Quebec, and southern Ontario are commonly smooth, whereas specimens from the southeastern part of the range are exclusively smooth (Table 2, Fig. 19).

Elytral colouration is more complex than is rugosity: females show three states -- vittate, fasciate, and non-fasciate; males show two states -- fasciate and non-fasciate. The vittate condition is characterized by marginal stripes, transverse basal fasciae and from two, but commonly eight to ten, narrow longitudinal vittae (Fig. 9). The fasciate condition is characterized by stripes and basal fasciae only (Fig. 8). The non-fasciate condition is characterized by marginal stripes only. The degree of concentration of the three female conditions in each geographic area ranges from: vittate -- 59% in New England, New York, and Pennsylvania to 80% in Manitoba and Saskatchewan; fasciate -- 5% in northwestern U.S.A. and British Columbia to 36% in midwestern U.S.A.; non-fasciate -- 3% in midwestern U.S.A. to 21% in northwestern U.S.A. and British Columbia. The fasciate condition for males ranged from 91% in northwestern U.S.A. and British Columbia to 64% in midwestern U.S.A. (Table 2, Fig. 19). There is some correlation between the abundance of fasciate males and vittate females within areas, throughout the range. In specimens from northwestern U.S.A. and British Columbia 91% of males were fasciate and 74% of females were vittate. About half of males from Alberta were fasciate and about half of females were vittate. In specimens from Michigan, two-thirds of males were fasciate and two-thirds of females were vittate.

Natural history notes. – Galewski (1964, 1971) presented evidence that adults of European *Hydaticus* overwintered out of water as they were found in forest debris or litter. Preliminary evidence for *H. modestus* indicates a similar pattern; for instance, adults from Framingham, Massachusetts were labelled "by sifting", and "under stone, high dry hill" and were collected in January, March and April. Specimens from Arlington, Massachusetts were labelled "moss roots" and were taken in March and December. Fletcher and Gibson (1908) recorded specimens from moss but did not give time of year. A specimen was collected 13.ix.79 in leaf litter at George Lake, Alberta approximately 3 m from water line.

Flight records are 13.iv.24 at Framingham, Massachusetts; 21.vi.08 at Algonquin, Illinois; 30.viii-3.ix.69 at Chaffey's Locks, Leeds Co., and 14.ix.73 at Harrow, Ontario; 3.vi.75 at St. Cloud and 1.ix.70 at Itasca State Park, Minnesota, and 29.ix.56 at Creston, British Columbia. Although these records are few, the general indication is of two major periods of flight, spring and fall, perhaps indicating pre- and post-overwintering movements. However, it is also possible that these beetles were intercepted during flight to temporary ponds or between ponds. A number of specimens were recorded by Hatch (1924) as occurring in beach drift in Charlevoix Co., Michigan.

Larson (1975) noted that *H. modestus* was found most commonly in the forested regions of Alberta. Adults were taken in dense detritus, or emergent vegetation along margins of ponds. The senior author has taken them in similar situations in Ontario. In Mer Bleu marsh, near Ottawa, specimens were collected among emergent *Carex*, in the drainage ditch of a small beaver pond. Near Moffat, Halton R.M., Ontario, specimens were collected among dead *Typha* leaves of a permanent woodland pool on 24.iii.76. Andrews (1923) collected adults by dredging aquatic plants at Whitefish Point, Chippewa Co., Michigan. James (1970) included *H. modestus* in his key to the aquatic beetles of vernal woodland pools in Hastings Co., Ontario. Mature larvae of *H. modestus* were described by Watts (1970) (as *H. stagnalis*) but the adequacy of this description was criticized by Galewski (1975). Records for teneral adults are: 24.vi.33 at Beach, Illinois; 10.viii at L'Anse, Michigan; 14.vii.27 at Long Beach, Long Island, New York; 12.vii.56 at Chatterton, 2.vii.19 at Port Stanley and 4.vii.57 at Spanish, all in Ontario.

Larson and Pritchard (1974) suggested that, for the males, there was a stridulatory function for the dorsal surface of the expanded protarsi and the accompanying pegs on the protibiae.

Distribution. – Map, Fig. 20. In North America, this species is transcontinental and ranges as far south as California, Missouri, and the New England states. Zaitzev (1953) recorded *H. rugosus* from Ust'-Aldan, Yakutsk, Bulun, and Irkutsk, in Siberia, U.S.S.R. As well as the type of *H. rugosus*, the following specimens from the U.S.S.R. were examined: Sibir oc., Barnaul am Ob, v.20, leg. Babiy, (CUIC), 2; Barnaul am Ob, 25.iv.18, Babiy, (CUIC), 1.

Chorological relationships. – *H. modestus* is sympatric with *H. piceus* in northeastern U.S.A. and from Alberta to Quebec in Canada. Possibly, *H. modestus* is sympatric with *H. continentalis* in Siberia, U.S.S.R. (Zaitzev, 1953).

Phylogenetic relationships. – *H. modestus* is more closely related to a complex of Palaearctic *Hydaticus*, centering around *H.* continentalis, than it is to other Nearctic *Hydaticus*.

Material examined. – The number of specimens examined was 378 ♂♂, and 500 ♀♀.

Hydaticus (*Hydaticus*) *piceus* LeConte

Figs. 1, 2, 21-27. Distribution map, Fig. 28.

Hydaticus piceus LeConte, 1863: 23. -- Crotch, 1873: 404. -- Sharp, 1882: 653. -- Wickham, 1895: 150. -- Beaulne, 1917: 125.
Hydaticus piceous Gordon and Post, 1965: 23, misspelling.

Notes on synonomy and type material. – LeConte, in the original description, gave a general description of the distribution as "Middle States and Canada", but did not give a specific locality. The holotype is a male in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. It is labelled as follows: Ill.; Type 6086 (red label).

Diagnostic combination. – The predominantly reddish-brown colour, absence of elytral stripes, shape of the median lobe and epipenite of the aedoeagus of males distinguish members of this species. Adults of *H. piceus* have been confused, in collections, with those of *H. cinctipennis*. The former are distinguished by smaller size, more oval shape, and lack of sub-lateral stripes and basal fasciae.

Description. – Length 11.6 to 14.0 mm, width 6.6 to 7.9 mm, other measurements in Table 1. Form oval, moderately convex. General colour reddish-brown. Head yellowish to piceous posteriorly; infuscation of frons generally in form of inverted "Y" (Fig. 21), but in some specimens joined by indistinct, fuscous areas extended inward from eyes in the form of indistinct maculae. Pronotum yellowish to dark brown, lighter laterally, often with baso-central infuscation or blotches (Fig. 22). Elytra yellowish to dark reddish-brown, with small, isolated, obsolete irrorations; irrorations denser basally and laterally; lateral, yellow stripes absent, but lateral, yellowish margin present or absent, when present indistinctly delimited (Fig. 22). Ventrally, prosternum lightest in colour, yellow to yellowish-red; remainder of thorax piceous to black; abdominal sterna intermediate in colour, some specimens with yellow maculations laterally. Profemora and mesofemora of many specimens yellowish with infuscations, tibiae and tarsi usually darker. Hind legs corresponding to abdominal colour. Rugosity, baso-laterally on elytra and laterally on pronotal disc of females, shallow, and in some specimens reduced to isolated, elongated depressions. Anterior metatarsal claw abruptly bent before tip, posterior claw with tip deflexed. Median lobe of aedoeagus moderately long ($\bar{x} = 2.8$ mm, N = 10), rounded basally; apex of median lobe, in side view, with projection (Fig. 24). In ventral view, lateral flanges narrow and extending almost to tip, apex of median lobe not modified (Fig. 25). Epipenite with lateral arms about two-thirds of the length of median arm (Fig. 26). Parameres narrow, acute at apex, with narrow, translucent flange on apical half (Fig. 27).

Variation. – Colour of adults varies markedly. Many samples from single localities exhibit extremes of colour, although specimens from Ontario and Quebec are consistently darker. Presence or absence of marginal, yellowish area of the elytra is not related to geographic localities. This yellow area contrasts markedly in many adults with colour of the suture but colours evenly intergrade between the suture and the lateral margin.

Natural history notes. – Needham and Williamson (1907) recorded adults of *H. piceus* from a permanent spring-fed pond at Lake Forest, Illinois where they were taken among *Typha* stalks in water as deep as 1 m. Sherman (1913) supported this record in his discussion of Dytiscidae of meadow ponds. Adults were recorded at large, coloured search-lights at Niagara Falls, Ontario by Stirret (1936). Only two other records of flight are available: St. Paul, 25.vi.21 and Albert Lea, 10.vii.23; both localities are in Minnesota.

During the fall of 1975 and spring of 1976 adults were observed near Moffat, Halton R.M., Ontario. The habitat was a permanent woodland pool with deep, organic detritus and diverse flora of aquatic vascular plants. In September and October, 1975, adults of *H. piceus*, assumed to be newly emerged, were collected among emergent *Carex*. In April and May of 1976, specimens were collected consistently among *Typha* stalks. In the laboratory, females oviposited into the leaf petioles of *Alisma plantago-aquatica* L. (Alismaceae). Eggs hatched after about two weeks and the larvae were fed on mayfly naiads and mosquito larvae collected from the pond. Larvae of *H. piceus* are agile swimmers and were observed to frequent open water as well as dense vegetation in the laboratory and in pond situations.

Distribution. – Map, Fig. 28. The general range of this species extends from central Alberta and southern Manitoba southward to Missouri, eastward to the New England states and northward into Quebec. The Alberta locality (Sturgeon River at bridge 2mi. N.W. of Calahoo, 1.vi.77, K.A. Shaw, in *Myriophyllum* sp. at river edge, [(UASM), 3♂♂] was unexpected since the most westerly previous record had been Winnipeg, Manitoba. This species was not found during the extensive survey by Larson (1975). Subsequently, specimens from Buchanan, Hudson Bay and Prieceville, Saskatchewan (SPMC) were examined, indicating a sporadic, localized distribution of this species along the southern edge of the boreal forest of western Canada.

Chorological relationships. – *H. piceus* is sympatric with *H. cinctipennis* in the more southerly part of its range. It is also sympatric with *H. modestus* in northeastern United States, and in Alberta, Manitoba, Ontario, and Quebec in Canada.

Phylogenetic relationships. – This species could be closely related to *H. cinctipennis*; however, the shared derived characters uniting these two species are relatively weak. As well, the relationship of these two species to other *Hydaticus* is obscure.

Material examined. – The number of specimens examined was 169 ♀♀ and 206 ♂♂.

Hydaticus (*Hydaticus*) *cinctipennis* Aubé

Hydaticus cinctipennis Aubé, 1838: 191, 192. -- Sharp, 1882: 651. -- Zimmermann,1919: 225. --Wallis, 1939: 127.

Notes on synonomy and type material. – The type-area specified by Aubé was the United States and the Antilles.

Mr. J.T. Huber kindly searched for the type of *H. cinctipennis* in various European museums, including the Aubé and Dejean collections of the Paris Museum, the collections of the National Museum of Belgium, Brussels, and those of the British Museum of Natural History, London, but without success.

H. cinctipennis has been a source of taxonomic confusion, possibly because of its rarity in collections. Wallis (1939) hesitated to synonomize this name with that of *H. modestus* because he had not seen specimens which agreed exactly with Sharp's (1882) description and because Zimmermann (1919) considered *H. cinctipennis* to be valid. Aubé's original description does seem to apply very well to the specimens studied although the type series was not located.

Diagnostic combination. – Large size, predominantly reddish-brown colour, short but distinct, yellow, sub-lateral stripes on the elytra and form of male aedoeagus distinguishes adults of this species from others of the genus in North America.

Description. – Length 12.8 to 14.7 mm, width 6.9 to 7.6 mm, other measurements in Table 1. Form ovate, moderately convex. General colour reddish-brown. Frons yellowish-brown to dark-brown posteriorly, infuscation irregular but in form of indistinct maculae posteriorly in some specimens (Fig. 29). Pronotum of most specimens lighter laterally, some with baso-central infuscation (Fig. 30). Head and pronotum of some specimens unicolourous, yellowish-orange. Elytra reddish-brown to dark brown; sub-lateral, yellow stripes distinct, not recurved suturally at base, marginal basally but curved away from margin posteriorly, ending from two-thirds to three-quarters of elytral length; area between stripes and outer margins darker; transverse fasciae present (Fig. 30) or absent at base. Ventrally, prosternum lightest in colour, yellowish to yellowish-brown; remainder of thorax dark reddish-brown to black; abdominal sterna of many specimens darkest, some with yellow maculations laterally. Profemora and mesofemora of many specimens yellowish with infuscations, tibiae and tarsi of same colour or darker apically. Hind legs corresponding to abdominal colour. Rugosity absent, or on females: baso-laterally on elytra and laterally on disc of pronotum, shallow and, on some specimens, reduced to isolated, elongate depressions. Anterior metatarsal claw about 0.40 length of posterior claw, both slightly bent at tip, anterior claw more acutely bent in females than in males. Metatibiae ventrally with row of spines only slightly curved inward at base (Fig. 31), but not as noticeably as in adults of subgenus *Guignotites*. Median lobe of aedoeagus long $\bar{x} = 3.3$ mm, $N = 5$), broadly rounded basally, apex acutely angled in side view (Fig. 32). In ventral view, lateral flanges ending well before tip, median lobe broadened apically (Fig. 33). Epipenite with lateral arms about same length as median arm but extending apically less than half the length of median arm (Fig. 34). Parameres broad, with wide, translucent, membranous flange on posterior half (Fig. 35).

Variation. – Specimens from southern United States (Florida, Georgia, Mississippi) are smaller than more northern specimens (Table 1). Also, the head and pronotum of southern specimens are more uniformly orangish in marked contrast with darker, elytral colour. Elytra of most of the northern specimens are more uniformly coloured with respect to pronotal colour.

Transverse fasciae at the base of the elytra were evident in 7 of 45 specimens examined. Fasciae are isolated, pale spots near the base, or full, distinct transverse bands as in Figure 30. Presence or absence of fasciae was not related to the sex of the specimen.

Natural history notes. – Immature stages of *H. cinctipennis* are unknown. Habitat of adults is also unknown.

Distribution. – Map, Fig. 28. The general distribution of *H. cinctipennis* is inferred from scattered localities as being the Atlantic coastal plain from New York south to Florida and west along the Gulf coastal plain to Mississippi, and north in the Mississippi River valley to Tennessee.

Aubé (1838) wrote that he had seen a specimen from the Antilles. This is an interesting record since no other North American species of *Hydaticus* (*s. str.*) shows a tendency toward toleration of brackish-water situations which would be useful in colonizing and exploiting aquatic habitats within the Antilles. The only species of *Hydaticus* known with certainty from the Antilles are in the subgenus *Guignotites*, and these occur commonly in brackish water. Fleutiaux and Sallé (1890, p. 352) provided a possible explanation for this anomaly. Félix Lhérminier collected extensively in Guadeloupe and in South Carolina and, upon his death, his collections were sent to Chevrolat and Dupont. The collections, however, were mixed and certain species from the U.S.A. were labelled as if they had come from Guadeloupe. Aubé (1838, p. viii-ix) acknowledged use of Chevrolat and Dupont collections. Therefore, it is possible that the specimen(s) Aubé recorded from the Antilles actually came from South Carolina, U.S.A. which is well within the known range of *H. cinctipennis*.

Chorological relationships. – This species is sympatric with *H. piceus* in the northerly part of its range and with *H. bimarginatus* in the southern and southeastern United States.

Material examined. – The number of specimens examined was 23 ♂♂ and 22 ♀♀ from the following localities:

UNITED STATES OF AMERICA

CONNECTICUT. Middlesex Co.: Cockaponsett St. Forest, 24.v.49, G.E. Pickford, fire pond, s. section, (PMNH), 1.

DELAWARE. Sussex Co.: Glasgow, 29.vi.53, 30.viii.50, H.E. Milliron, electric light, (UDCC), 2; Rehoboth Beach, -.viii.34, (ICCM), 1.

FLORIDA. Baker Co.: near Manning, xii.30.47, F.N. Young, (FNYC), 1. Walton Co.: near Bruce on Fla. Hwy. 20, x.17.41, F.N. Young, hog wallow, (FNYC), 1.

GEORGIA. Clinch Co.: 2.6 mil. W. Clinch Co.-Ware Co. line on Hwy #177, 8.vi.75, G.W. Wolfe, (GWWC), 1. Lowndes Co.: (county record only), v.13.63, E. Hazard, (OSUC), 1. Pierce Co.: Blackshear, viii.17.50, P.J. Spangler, (USNM), 1.

MASSACHUSETTS. (state record only), (ICCM), 1. Bristol Co.: Dartmouth, 20.x.06, (MCZC), 1; Fall River, iv.19.18, N.S. Easton, (CNIC), 1; Freetown, viii.16.12, N.S. Easton, (CASC), 1; No. Attleboro, 6.ix.20, C.A. Frost, (MCZC), 1; Westport, iv.18.03, (MCZC), 1. Middlesex Co.: Lexington, 20.iv.30, Darlington, (MCZC), 1. Norfolk Co.: Brookline, (MCZC), 1; Stoughton, -.vii.20, Blake, (USNM), 1.

MISSISSIPPI. Jackson Co.: Ocean Springs, vi.14.31, H. Dietrich, (CUIC), 1.

NEW JERSEY. Atlantic Co.: Atlantic City, 7.4.01, (USNM), 1. Burlington Co.: Atsion, vi.11.45, J.W. Green, (CASC), 1. Morris Co.: Great Swamp at end of White Bridge Rd., 2.ix.75, G.W. Wolfe, (GWWC), 1.

NEW YORK. Richmond Co.: Staten Island, (USNM), 2, (MCZC), 1, -.vii.91, iv.16.05, -.viii.25, (USNM), 3, iv.16-05, E. Shoemaker, (USNM), 2; Bull's Head, 1.4.21 (UASM), 1. Suffolk Co.: Long Island, M.L. Linell, (USNM), 1; Forrest Park, v.21.04, (USNM), 1; Orient, ix.3.49, R. Latham, (CUIC), 2; Riverhead, vi.5.36, vi.9.36, R. Latham, (CUIC), 2.

PENNSYLVANIA. Somerset Co.: Windber, 8.xi.24, (ICCM), 1.

RHODE ISLAND. Newport Co.: Tiverton, v.8.09, (MCZC), 1.

SOUTH CAROLINA. Charleston Co.: McClennanville, 2-3.vi.73, R. Turnbow, lite, (UMRM), 1.

TENNESSEE. White Co.: Swamp along Rt. 42, 7 mi. N. Sparta, 19.vi.76, G.W. Wolfe, (GWWC), 2.

VIRGINIA. Nansemond Co.: Dismal Swamp, iv.16-17.65, P.J. Spangler, (USNM), 2; Holland, vi.20.55, (JFMC), 1.

Subgenus Guignotites

Subgenus *Guignotites* Brinck, 1943: 141, new name for subgenus *Isonotus* Houlbert, 1934: 124, preoccupied by Lepeletier and Serville, 1828 (Coleoptera: Scarabaeidae). -- Guignot, 1950: 104. -- Franciscolo, 1968: 48.

Diagnostic combination. – Frons piceous to black basally; yellowish anteriorly, with or without distinct maculae (Figs. 47, 36). Pronotum with postero-lateral corners sharply and distinctly acute, posterior pronotal margin strongly sinuate and recurved laterally (Figs. 37, 43, 48 and 49). Row of spines on disc of posterior surface of metatibiae curved inward basally, not parallel to outer tibial margins (Figs. 38, 50). Elytra black; lateral and sub-lateral stripes present in most specimens, fused in some specimens to form a single, wide lateral band. Elytra with increased yellow ornamentation in some specimens (Fig. 48). Epipenite of male genital capsule on same side of preputial cover as median lobe; lightly sclerotized.

Hydaticus (*Guignotites*) *bimarginatus* (Say)

Figs. 36-45. Distribution map, Fig. 46.

Dytiscus bimarginatus Say, 1831: 5. -- Say, 1834: 442. *Hydaticus bimarginatus*, LeConte, 1869: 556. -- Crotch, 1873: 404. -- Sharp, 1882: 654. -- Blatchley, 1910: 233. -- Leng and Mutchler, 1918:89. -- Blatchley, 1919: 314. -- Young, 1954: 113. -- Matta and Michael, 1977: 48. *Hydaticus fulvicollis* Aubé, 1838: 184. *Hydaticus rimosus*? Young, 1954: 113; *nec* Aubé, 1838: 182.

Notes on synonomy and type material. – Say's type area is "Louisiana" but the types were lost (Le Conte, 1869a, p. VI). However, specimens in the LeConte collection, MCZC, are considered characteristic of Say's species (Lindroth and Freitag, 1969). A male from the LeConte collection is hereby designated as NEOTYPE (MCZC type number 32443). It bears an orange, circular label (for southern States), and another label "*bimarginatus* 4". It is well within the range of variation described by Say. It lacks the left mesotibia and mesotarsus, and claws of the left metatarsus. A neotype is needed to clarify the concept of this taxon because of the similarity to *H. rimosus* and because the type of *H. rimosus* was not found. Aubé (1838) recorded the type area of *H. rimosus* as the United States, but type material was not located.

The most commonly cited original description of *H. bimarginatus* is that of Say (1834). This is possibly because the 1834 description is the one quoted by LeConte (1869b). However, Scudder (1899) discussed a paper written by Say in 1831 which contained the description of *Dytiscus bimarginatus* (see also Bequaert (1951) and Leech (1970, p. 241, footnote 1).

In the original description, Aubé suggested that *H. fulvicollis* could be identical to *H. bimarginatus*. Subsequent authors have considered the names to be synonymous. Because Aubé gave a general description of the distribution as the United States and because *H. bimarginatus* is the only similar species in the type area, the two are considered synonymous herein, although the type of *H. fulvicollis* was not located.

Specimens from Broward Co., Florida, which Young (1954) identified as "*H. rimosus*? " because of their colour pattern, are similar to a few other specimens from Texas, Louisiana, Maryland, and Virgina. However, shape of apex of median lobe of the aedoeagus and number of large spines on the metatibiae places them within the limits of *H. bimarginatus* as interpreted here.

Young (1954) suggested that *H. rimosus* and *H. bimarginatus* could be subspecies. This could be so, for there is extensive overlap in colour pattern and a close similarity in other morphological characters. However, *H. rimosus* and *H. bimarginatus* are considered specifically distinct because of subtle, yet consistent, morphological differences. In addition, there was a small area of sympatry within the West Indies.

Sharp (1882) noted differences in body shape of *H. bimarginatus* and *H. rimosus*. The pronotum of *H bimarginatus* is more abruptly curved outward at the anterior projections and the elytra are less distinctly widened post-medially. The pronotum of *H. rimosus* is more linear from the anterior projections to the base and the elytra are distinctly widened post-medially. In dorsal profile the sides of *H. bimarginatus* are more parallel than those of *H. rimosus*. These differences are noticeable in the sympatric specimens from Cuba; however, these differences

Table 3. Variation in number of large spines on anterior (lower) surface of left (SLT) and right (SRT) metatibiae of selceted samples of North American taxa of *Hydaticus (Guignotites) (Coleoptera: Dytiscidae)*

			SLT			*SRT*		
Taxon	Locality	Sex	N	Mean	Range	N	Mean	Range
H.bimarginatus	Dismal Swamp, Va.	♂	10	12.4	10-14	10	11.9	10-15
		♀	10	12.3	11-15	10	11.9	10-15
	Highlands Co., Fla.	♂	10	13.0	12-15	10	12.6	11-15
		♀	10	11.9	9-17	10	12.5	11-16
	Texas	♂	10	12.5	10-16	10	13.0	11-14
		♀	10	11.6	10-14	10	12.2	10-14
	Cuba	♂	1	11.0		1	12.0	
		♀	5	10.4	9-12	5	11.8	10-13
H. rimosus	Cuba; Bahamas, B.W.I.	♂	9	6.7	5-8	5	7.0	6-8
		♀	5	6.6	6-7	5	5.8	5-7
	Mexico; Guatemala; Br.Honduras; Honduras	♂	14	6.7	5-8	14	6.7	5-9
		♀	15	6.6	5-9	13	6.7	2-9

are too subtle to be used as diagnostic characters.

Diagnostic combination. – Adults of this species are recognized by combination of the following characters: small size, undeveloped sub-lateral, elytral stripes, average of more than ten large spines on lower disc of metatibiae, and angulate tip of median lobe of aedoeagus.

Description. – Length 10.9 to 13.1 mm, width 5.8 to 7.2 mm, other measurements in Table 1. Form ovate, moderately convex. General colour black. Clypeus and frons yellowish to yellowish-red, except posterior, transverse black band and antero-lateral projections (Fig. 36), some specimens with maculae on frons enclosed by black areas. Pronotum yellowish to yellowish-red, except for transverse, black band at base; band not extended to lateral margins, band as wide as distance between inner limits of basal, recurved portions of elytral stripes and restricted to basal third in most specimens (Fig. 37), but in some specimens extended as a narrow band to anterior border. Elytra piceous to black; lateral and sub-lateral, yellow stripes distinct; lateral stripes marginal, separated from sub-laterals or joined to them in many specimens, in most specimens originating in basal third and ending sub-apically with yellow lobes (Fig. 37) and/or spots; sub-laterals recurved suturally at base, sub-marginal at base, but curved inward from margin posteriorly, ending from two-thirds the length of elytra to near apex of elytra, medial and post-medial, sutural extensions of yellow absent; yellow transverse, basal fasciae absent. Ventrally, prosternum lightest in colour, yellow to yellowish-red; remainder of thorax black; abdominal sterna piceous to black. Profemora and mesofemora yellow with varied amounts of infuscation, tibiae more infuscated, tarsi darkest. Hind legs piceous to black, corresponding to adominal colour. Rugosity of pronotum of females absent or, in most specimens, in form of isolated, circular areas not in contact with anterior or lateral borders of pronotum (Fig. 43); rugosity of elytra absent from most specimens but in some in form of elongate, shallow depressions baso-laterally. Anterior metatarsal claw about half the length of posterior claw, both claws bent downward at tip (Fig. 44), anterior more so in females than in males. Anterior disc of metatibiae with large spines (Fig. 45), ($\bar{x} = 12.2$, max. = 16, min. = 8, N 1 150). Median lobe of aedoeagus short ($\bar{x} = 2.0$ mm, N = 10), unevenly rounded basally, apex, in side view, angulate (Fig. 39). In ventral view, lateral flanges ending sub-apically, apex of median lobe not modified (Fig. 40). Epipenite with lateral arms extending about two-thirds the length of median arm, narrowed apically; median arm wide, rounded at tip, thickened medially (Fig. 41). Parameres narrow, acute at apex, with narrow, translucent flange on apical third (Fig. 42).

Variation. – Adults are quite variable with respect to form of lateral, and sub-lateral elytral stripes and amount of darkening of pronotum. Most specimens have yellow marginal stripes beginning at about one-third of elytral length and extending to apex or ending sub-apically. Lateral stripes on some specimens have two to four apical extensions of yellow, although these are reduced to isolated spots in a few specimens. Sub-lateral stripes of most specimens have inner margins curvilinear and in some specimens these stripes are abruptly narrowed, usually at about two-thirds of elytral length. Inner edges of sub-lateral stripes are uneven in some specimens but distinct median and post-median sutural extensions of yellow are absent. In some specimens, lateral and sub-lateral stripes are united as a single, broad, lateral band (Fig. 37).

Black colour at base of pronotum is relatively uniform in width but varies markedly in length. In most specimens, it is restricted to the basal third (Fig. 37), but in some it extends as much as three-quarters of pronotal length as a broad, semi-lunar area, or as a narrow, black band from wide, basal area to anterior margin. Black area does not extend the entire length of the pronotum as a wide, black band as in some specimens of *H. rimosus* (Fig. 49). Commonly, the frons is immaculate (Fig. 36), but inward, lateral and central, anterior infuscations enclose indistinctly defied maculae. These infuscations vary in darkness and in very few specimens approach the wide, black area seen in *H. rimosus* (Fig. 47).

Number of large spines on disc of lower surface of metatibiae (Fig. 45) varies from nine to 18, with the average consistently greater than 10 in more than 150 specimens examined. In addition, males with an average of 10 to 12 spines were found to have the tip of median lobe of aedoeagus angulate in side view. Numbers of large spines on left and right metatibiae of specimens used for descriptive measurements are presented in Table 3.

Natural history notes. – Young (1953, 1954) noted that most specimens were found in clear temporary fresh-water ponds, but also recorded occurrence of a few specimens in brackish-water habitats. Young (1954) regarded *H. bimarginatus* in Florida as an erratic occupant of the lowland and upland regions, but noted that it was more abundant in flatwoods situations.

Matta (1973) found adults of *H. bimarginatus* in woodland pools and in thick vegetation of non-acidic, fresh-water ditches, also beetles were collected in a deep, permanent, sand-bottom pool with no vegetation and in a small bog characterized by large clumps of *Typha latifolia* L. and *Juncus effusus* L. in the Dismal Swamp of Virginia.

Label data indicate a wide variety of aquatic habitats, from saline (brackish pools, brackish water, salt marsh), to permanent (woods pond, tupelo swamp, sink hole pond), to temporary or disturbed (canal, pool in canal, puddle in forest stream, temporary pond). Judging from the frequency of specimens labelled "electric light", "black light", and "black light trap", ranging from February to November, adults of this species apparently come to light more readily than those of any other North American species of *Hydaticus*. Eggs, larvae, and pupae are undescribed.

Geographical distribution. – Map, Fig. 46. The general range of this species includes the Atlantic and Gulf coastal plains of the U.S.A. (New York south to Florida and west to Texas) and parts of the West Indies.

Chorological relationships. – *H. bimarginatus* is sympatric with *H. cinctipennis* over the whole range of the latter; and with *H. piceus* in the northern part of the Atlantic coastal plain. It is sympatric with *H. rimosus* in Cuba and the Bahama Islands, however, no zone of sympatry with *H. rimosus* was found on the continent. More intensive collecting along either side of the Mexico-U.S.A. border should provide valuable information.

Phylogenetic relationships. – *H. bimarginatus* and *H. rimosus* are sister species that represent an invasion from the Neotropical realm.

Material examined. – The number of specimens examined was 331 ♂♂, and 313 ♀♀.

Hydaticus (*Guignotites*) *rimosus* Aubé

Figs. 3, 47-56. Distribution map, Fig. 46.

Hydaticus rimosus Aubé, 1838: 182, 183. -- Chevrolat, 1863: 202, 203. -- Sharp, 1882: 654.

Notes on synonomy and type material. – Aubé's type of *H. rimosus* was not located. In his original description he stated that *H. rimosus* was found in Mexico and the Antilles. He included a possible record for Paraguay.

As interpreted here, *H. rimosus* does not occur in continental U.S.A. *H. stagnalis* of Horn (1894) and *H. bimarginatus* of Horn (1896) from San José del Cabo, Territory of Baja California, Mexico are most likely variants of *H. rimosus* with less developed markings of the sub-lateal stripes (Leech, 1948).

Diagnostic combination. – Adults are recognized by combination of: small size, often highly developed sub-lateral elytral stripes, average of less than ten large spines on lower disc of metatibiae, and truncate tip of median lobe of aedoeagus.

Description. – Length 11.1 to 13.7 mm, width 6.2 to 7.0 mm, other measurements in Table 1. Form ovate, moderately convex. General colour black. Head black except clypeus and two, large, oval maculae on frons, yellowish to yellowish-red (Fig. 47). Pronotum yellowish to yellowish-red, except transverse, black band at base; band not extended to lateral margins, in most specimens as wide as distance between inner limits of basal, recurved portions of elytral stripes; in many specimens extending anteriorly as a broad, black band (fig. 49), and in some specimens enclosing a broad area of anterior margin. Elytra piceous to black; lateral and sub-lateral yellow stripes distinct, lateral stripes marginal, separated from sub-laterals in some specimens or both stripes joined, originating in basal third in most specimens and ending sub-apically with yellow lobes (Fig. 48) and/or spots; sub-lateral stripes sub-marginal at base, recurved suturally, and curving away from margin posteriorly (Fig. 49), ending from two-thirds the length of elytra to near apex, inner edges of sub-lateral stripes undeveloped (Fig. 49), or with sub-basal, inward extensions connected with basal, transverse fasciae, and in a few specimens with medial and post-medial lobes of yellow present as only isolated spots, lobes as wide as stripe in most specimens (Fig. 48); yellow, transverse, basal fasciae present (Fig. 48) or absent (Fig. 49). Ventrally, prosternum lightest in colour, yellowish to yellowish-red; remainder of thorax black; abdominal sterna piceous to black. Profemora and mesofemora yellowish-red with variable amounts of infuscation, tibiae more infuscated, tarsi darkest. Hind legs piceous to black, corresponding to abdominal colour. Rugosity, in most specimens, restricted to pronotum of females; varying from small isolated areas laterally to broad bands from anterior to posterior margins, in most specimens not involving lateral margins. Anterior, metatarsal claw about half the length of posterior claw, bent downward at tip in females but not in males (Fig. 55). Anterior disc of metatibiae with average of less than ten large spines (Fig. 56), $\bar{x} = 6.7$, max. = 10, min. = 2. N = 42). Median lobe of aedoeagus short $\bar{x} = 2.2$ mm, N = 5), unevenly rounded basally, apex truncate in side view (Fig. 51). In ventral view, lateral flanges ending sub-apically, apex of median lobe not modified Fig. 52). Epipenite with lateral arms sub-equal to or slightly longer than median arm, rounded apically; median arm wide, rounded at apex, thickened medially (Fig. 53). Parameres narrow, acute at apex, with narrow, translucent flange on apical half (Fig. 54.)

Variation. – No specimens of *H. rimosus* included in this study were without distinct maculae on the frons. Most had two anterolateral projections of black from the lower band of maculae (Fig. 47). Size of the black area at base of pronotum was usually greater in *H. rimosus* than in *H. bimarginatus*. In most specimens of *H. rimosus*, the length of the black area is greater than one-half of pronotal length, ending sub-apically in most specimens (Fig. 48), and in some specimens involving width of pronotum posterior to head. Lateral and sub-lateral yellow elytral stripes are extremely varied in size and extent (compare Figs. 48, 49). Specimens with the least developed stripes resemble those of *H. bimarginatus*. Basal recurved portions of sub-lateral stripes, in a few specimens, have short, posterior prolongations. The area between basal, recurved portions and sub-basal, inward extensions, in some specimens, is also yellow. Sub-basal inward extensions of yellow and basal transverse fasciae vary from complete and distinct, to isolated spots, to obscure yellowish-brown areas. Lateral and sub-lateral stripes, in a few specimens, are joined as wide, lateral stripes, much as in some specimens of *H. bimarginatus*, however, in *H. rimosus* the wide stripes are usually accompanied by yellow ornamentation. Apical portions of lateral stripes are dilated in most specimens (Fig. 48).

As in *H. bimarginatus*, the number of large spines on disc of the lower surface of metatibiae (Fig. 56) varies appreciably. However, there are limits between the two species. Although some tibiae have only two, others have 10 spines, the average number of spines per tibia of the specimens observed was consistently less than 10 (Table 3).

Natural history notes. – The immature stages of *H. rimosus* are undescribed and very little is known about the habitat of the adults. Specimens from Nayarit, Mexico were labelled "pool in drying stream bed" and "pool in stream". Adults were collected at light in late July and early August in Sinaloa, Mexico.

Geographical distribution. – Map, Fig. 46. This species is found in the Antilles, Mexico, and southward to at least Honduras. Aubé's record of *H. rimosus* from Paraguay is based on a single female specimen with a smooth pronotum. This could represent a distinct taxon as Aubé (1838: 184) suggested because in this study no specimens of *H. rimosus* were received from south of Honduras, but of those received from other areas, the pronotum of at least a few females was smooth.

Chorological relationships. – *H. rimosus* could be a southern sub-species of *H. bimarginatus* as suggested by Young (1954) because differences between adults of the two species are subtle. Intermediate specimens have not been discovered; however, too few specimens were seen from northern Mexico to indicate zones of contact. The two species appear to be sympatric in Cuba and the Bahama Islands.

Phylogenetic relationships. – *H. rimosus* and *H. bimarginatus* are closely related species that, in aggregate, have their closest relatives within the Neotropical Region.

Material examined. – The number of specimens examined was 37 ♂♂, and 35 ♀♀ from the following localities:

BAHAMAS, BRITISH WEST INDIES

NEW PROVIDENCE: 4 mi. SW Nassau, iv.8.53, E.B. Hayden, (FNYC), 1.

BRITISH HONDURAS

Punta Gorda, vii.34, (CASC), 1.

CUBA

CAMAGUEY: Camaguey, xii.20.23, J. Acuna, (UGIC), 2. LAS VILLAS: Buenos Aires, Trinidad Mts., v.8-14,36, Darlington, 2500-3500', (MCZC), 4. ORIENTE: Cuabitas, Stgo. de Cuba, v.51, P. Alayo, (UGIC), 1; Cauto El Cristo, (Cauto R.), viii.12.36, (UGIC), 1. Rangel Mts., P. de Rio, viii.24.36, Darlington, about 1500', (MCZC), 1. Upper Ovando R., vii.17-20.36, Darlington, 1000-2000', (MCZC), 1.

GUATEMALA

El Salto, Esquintla, .34, F.X. Williams, (FNYC), 1. Naranjo, El Petén, iii.20.22, H.F. Loomis, (FNYC), 1. Péten Tikal, iv.9.56, T.H. Hubbell & I.J. Cantrall, at light at camp, (FNYC), 1.

HONDURAS

DEPT. MORAZÁN: Zamorano, Esc. Agr. Pan., vii.6.48, T.H. Hubbell, 2600', (carbonál), (FNYC), 1.

MEXICO

(Country record only), (MUSC), 1. BAJA CALIFORNIA: betw. San José del Cabo and Triunfo, (CNIC), 1; San José del Cabo, Fuchs, (CASC), 1. CAMPECHE: Hopelchen, 18 mi. E., xi.28.63, K.L. McWilliams, (NMSU), 1. CHIAPAS: Chuatemoc, viii.28.63, K.L. McWilliams, (NMSU), 1. COAHUILA: Matamoros, .v., (CASC), 1. COLIMA: 30 mi. NE Colima, xii.4.48, H.B. Leech, (CASC), 2, (FNYC), 1; Colima, 20 mi. W., vi.6.63, K.L. McWilliams, (NMSU), 2. JALISCO: La Huerta, 6 mi. N., x.25.66, A.H. Smith & J.R. Zimmerman, roadside puddle, (NMSU), 2; La Huerta, 6 mi. N. & 2 mi. E., iii.22.71, J.R. Zimmerman, (NMSU), 1. NAYARIT: 24 mi. N. Acaponeta, vii.63, F.D. Parker & L.A. Stange, (UCDC), 1; 20.3 mi. W. Compostela, vi.19.67, A.R. Hardy, (UCRC), 1; Sierra de Zapotan, xi.42, E. Paredes, pool in stream, (CASC), 3; 20 mi. SE Tepic, 23.ix.48, pool in drying steam bed, (CASC), 3. OAXACA: Oaxaca, 20.vii.37, Embury, 3000', (CASC), 1. SAN LUIS POTOSI: N. Morelos, iii.21.59, (NMSU), 3; Paletla, xii.19.40, F.N. Young, (FNYC), 2; Tamazunchale, Quinta Chilla Cts., 19.vi.71, A. Newton, Trop. sub-evergreen for., ca. 600', blacklight trap, (INHS), 2. SINALOA: Coyatitan, 3 mi. E. on road to San Ignacio, iv.9.75, J.R. Zimmerman, (NMSU), 1; 5 mi. N. Mazatlan, vii.22.72, J. & M.A. Chemsak, A. & M.M. Michelbacher, (CISC), 1, vii.25.73, J. Chemsak, E.G. Linsley & A.E. Michelbacher, at lite, (CISC), 1, vii.26.73, J. Chemsak, at lite, (CISC), 1, vii.28.73, J. Chemsak, at lite, (CISC), 1, vii.29.66, J. Chemsak & J. Doyen, white lites, (CISC), 1, 30.vii.64, W.C. McGuffin, (CNIC), 2, viii.5.64, J.A. Chemsak & J. Powell, black and white lights, (CISC), 1, viii.5-7.64, H.F. Howden, (CNIC), 1. TABASCO: Villahermosa, 5 mi. S., viii.26.63, K.L. McWilliams, (NMSU), 3. TAMAULIPAS: ditch N. of Mante, vi.12.60, F.N. Young, (FNYC), 3. VERACRUZ: J.D. Covarrubia, 1 mi. N., viii.26.62, J.R. Zimmerman, (NMSU), 1; Lake Catemaco, D.C. Robinson, (TAMU), 4; 13 km. WNW Potrero, vii.16.48, H.B. Leech, (CASC), 1. YUCATAN: Chichen Itza, Xtolok Cenote, vi.28.32, E.P. Creaser, (MCZC), 1; Progreso, 3 mi. S., xi.24.63, K.L. McWilliams, (NMSU), 3.

SPECIES OF UNCERTAIN PLACEMENT

A female specimen of *Hydaticus (G.) grammicus* Germar, 1830, is labelled: FLA: Highlands Co.; Archbold Biol. Sta.; 13-x-1964; P.H. Arnaud, Jr., (CASC), Zaitzev (1953) reported this species from southern U.S.S.R., central and southern Europe, Iran, and Japan. The Florida specimen appears to be identical to specimens received from European collections. Most likely it is mislabelled but it could be an isolated occurrence of the species in North America. Leech (1970) discussed some intriguing additions to the California water beetle fauna which could have been introduced by means of aquaria supplies.

The name *Hydaticus riehli* Wehncke, 1876, was not associated with any specimens studied. The type locality is Cuba but the collection of the Academia de Ciencias, Havana, Cuba contained no specimens assigned to this name. Sharp (1882, p. 782) was of the opinion that the species belonged to *Thermonectus* Dejean.

PHYLOGENY

Introduction

Methods, principles, usefulness, and importance of cladistic analysis for extant faunas are presented by Hennig (1966), Brundin (1966), Ball and Erwin (1969), Erwin (1970), Whitehead (1972), Noonan (1973), and Kavanaugh (1972), 1978). Darlington (1970) and Ashlock (1980) discuss the limitations of cladistic techniques.

Cladistic techniques were used to discover relationships but the formal classification is not cladistic. Characters and character states used in phylogenetic analysis are presented in Table 4 and cladograms are presented as Figs. 57 and 58. Each character is numbered and the derived or apotypic state is represented by a filled circle on the cladogram. The ancestral or plesiotypic state is represented by an open circle. Characters which have three states are considered to have both a derived and a highly derived state; the last is designated by a prime mark(′).

An attempt to reconstruct the evolutionary history of a group, by cladistic techniques, employs analysis of transformation series (morphoclines) of two or more character states.

Table 4. Characters, character states, basis for polarity, and weight of characters used in phylogenetic analysis of the genera of Hydaticini, subgenera of *Hydaticus,* and species of *Hydaticus (s. str.)* (Coleoptera: Dytiscidae

Character	Character state		Basis for classification	Weight
	Plesiotypic	Apotypic		
Male Mesotarsal Acetabulum				
1. Brush on mesotarsomere 1	absent	present	ex	IV
2. Shape of brush	linear	group	in/ex	IIIa
3. Size of suckers	small	large, (′) very large	in	IIIb
4. Number of rows of suckers on mesotarsomeres 2 and 3	6	4, (′) 2	in/ex	IIIb
Hind legs				
5. Row of spines on metatibia	straight	curved	in/ex	IIIa
6. Metatarsal claws	equal	unequal	ex	IIIa
Elytra				
7. General colour	black	brown or yellow	in	IIIb
8. Basal fascia	present	absent	in	I
9. Longitudinal vittae	absent	present	in	IIIa
10. Longitudinal vittae/sex	both sexes	females only	in	IIIa
11. Lateral stripes	present	absent	in	I
12. Lateral and sub-lateral stripes	separate	fused	in	IIIa

(continued on next page)

Table 4 (continued)

Character	Character state		Basis for classification	Weight
	Plesiotypic	Apotypic		
13. Apical sinuation of females	absent	present	in	IIIa
14. Width of epipleuron	narrow	wide	ex	IIIa
Venter				
15. Colour	black	brown or yellow	in/ex	IIIa
Aedoeagus				
16. Position of epipenite	dorsal	ventral	ex	IV
17. Amount of sclerotization of epipenite	heavy	light, (′) absent	ex	II
		(′) absent	ex	I
18. Shape of epipenite	lateral arms as long as central arm	lateral arms shorter than central arm, (′) lateral arms much shorter than central arm	in	IIIb
19. Shape of epipenite	w	y	in	II
20. Width of ventral flange of paramere	narrow	wide	ex	II
Median Lobe				

(continued on next page)

Table 4 (continued)

Character	Character state		Basis for classification	Weight
	Plesiotypic	Apotypic		
21. Shape of tip	not swollen	swollen	in	IV
22. End-point of lateral flanges	sub-apical	apical in IIIa		
23. Terminal width of lateral flanges	narrow	wide	in	IIIa
24. Apex of median lobe in side view	parallel-sided	widened	in	IIIa

Polarity or direction of each morphocline is critical to an accurate reconstruction because taxa are grouped on the basis of apotypic rather than plesiotypic character states. Polarity of characters is often determined by frequency of occurrence. A character state distributed among all or most members of a monophyletic group is considered to have been present in the common ancestor of that group. Therefore, ex-group comparisons reveal the plesiotypic character state. Another technique, called in-group comparison, is used to establish modification and remodification of characters or polarity.

In determining the relationships of members of *Hydaticus (s. str.)*, distribution of character states within the subgenus must be known (in-group). Similarly, relationships within *Hydaticus (s. lat.)* require knowledge of character states within Hydaticini (ex-group). This should be supplemented by knowledge of character states among an immediate, higher taxon (ex-group, *viz.* Dytiscinae) such that an evaluation could be made of the number of times a character has been modified - i.e., group trends (Ross, 1974, p. 158). The manner in which character polarity was determined is given in Table 4.

All characters are not of equal value in reconstructing a phylogeny. For instance, gain of a character should be considered of more value than loss of a character, and gain of a complex, intricate character of more value than gain of a simple character. Ranking characters in terms of value for determining relationships is termed weighting. Character weighting allows separation of taxa which are similar because of parallel or convergent evolution. Hecht and Edwards (1976) proposed five weighting categories based on increasing information; a higher category indicating more information. Ball (1978) used a similar system for *Trichopselaphus* Chaudoir (Coleoptera: Carabidae).

The following list of types and characteristics of the weighting system is that of Ball (1978) modified slightly to apply to the character states present in Hydaticini.

I. Loss of a structure.
II. Simplification or reduction of a complex character.
III. Simple change, involving sclerotization, colour or position.
  a. Two states.
  b. Three states.
IV. Parts of a functional complex.

The weight of each character used in phylogenetic analysis of members of Hydaticini is given in Table 4. Specimens of taxa listed below were used for analysis, in addition to the North American taxa.

Prodaticus pictus Sharp
Hydaticus (*Hydaticus*) *bowringi* Clark
H. continentalis J. Balfour-Browne
H. (*H.*) *histrio* Clark
H. (*H.*) *seminiger* (Degeer)
H. (*H.*) *transversalis* (Pontoppidian)
H. (*H.*) *vittatus*-group
Hydaticus (*Hydaticinus*) *rectus* Sharp
Hydaticus (*Pleurodytes*) *dineutoides* Sharp
Hydaticus (*Guignotites*) *dorsiger* Aubé
H. (*G.*) *exclamationis* Aubé
H. (*G.*) *flavolineatus* Boheman
H. (*G.*) *fractivittis* Guignot
H. (*G.*) *grammicus* Germar
H. (*G.*) *leander* Rossi
H. (*G.*) *matruelis* Clark
H. (*G.*) *palliatus* Aubé
H. (*G.*) *subfasciatus* LaPorte

Analysis of Characters

Some of the characters used in the phylogenetic analysis require explanation because of possible alternate explanations of character transformation. The analysis would be greatly different if these character states were interpreted differently and therefore the reasons for one interpretation should be provided.

Mesotarsal acetabulum of male (characters 1, 2, 3 and 4, Figs. 2 and 3). – These characters could represent a functional unit, however, they do not show a direct, dependent relationship - *e.g.*, a large mesotarsal brush of the apotypic "group" state does not always occur in conjunction with larger mesotarsal suckers. Therefore, the characters are believed to have evolved independently and are weighted separately for phylogenetic analysis.

The presence of the brush on mesotarsomere 1 of male adults remains to be tested as a synapomorphy for all members of *Hydaticus (s. lat.)*. Franciscolo (1968) did not illustrate the mesotarsal brush of any species he studied, except *H.* (*G.*) *pullatus* Guignot (Fig. 14). However, the brush in the plesiotypic "linear" state is very difficult to see unless one is looking for it. For instance, an obscure, linear brush is present on the male mesotarsal palettes of *H.* (*G.*) *dorsiger*, *H.* (*G.*) *flavolineatus*, *H.* (*G.*) *grammicus* and *H.* (*G.*) *leander* even though it is not shown in Franciscolo's Figs. 20, 15, 17 and 10 respectively.

The size of suckers on the male mesotarsal acetabulum has been divided subjectively into three classes based on comparison of mesotarsal suckers to the smaller suckers of the protarsal palette. If the mesotarsal suckers were much smaller than the protarsal suckers they were classed as "small"; if they were slightly smaller than or equal to the protarsal suckers they were classed as "large"; and, if slightly larger than the protarsal they were classed as "very large". Perhaps these are not natural groups, but they do appear to be correlated with other characters in defining lineages.

The number of rows of suckers of the male mesotarsomeres 2 and 3 is difficult to analyze. Reduction of number of rows is not correlated to increasing size of individual suckers. In fact, the opposite trend appears -- decreasing number of rows and decreasing sucker size -- implying that the male mesotarsus has a different function or a difference in degree of function among some lineages of *Hydaticus (s. lat.)*.

Row of spines on venter of metatibia. – (character 5, Figs. 10, 23, 31, 38 and 50). The principal differences used by Guignot (1950) to distinguish *Guignotites* from other subgenera of *Hydaticus (s. lat.)*, was a "curved" (Figs. 38 and 50) rather than a "straight" (Figs. 10 and 23) row of spines ventrally on the metatibia. Members of *Pleurodytes* also possess the apotypic "curved" state of this character. However, possession of either state of this character is not definitive subgenerically because *H. cinctipennis* (Fig. 31), which belongs to *Hydaticus (s. str.)*, on the basis of a suite of other characters such as position, shape and degree of sclerotization of the epipenite, also possess a curved row of metatibial spines.

Vittae and apical sinuation of elytra (characters 9, 10 and 13, Figs. 7, 8, 9 and 18. – *H.* (*H.*) *continentalis* and *H.* (*H.*) *modestus* have forms in which the elytra are marked with longitudinal, yellow vittae. In *H.* (*H.*) *continentalis* most specimens of both sexes are vittate whereas in *H.* (*H.*) *modestus* only the female specimens are vittate although the percentage of population samples vary widely (Fig. 19). This sexual distinction is an example of divergent evolution which could be expected among predaceous water beetles which respond primarily to visual stimulae. At some time in the past, a complete distinction between the sexes with respect to vittae would be hypothesized - *i.e.*, females exclusively vittate. Females of some populations of *H. modestus*, as mentioned above, have now passed this intermediate state and become increasingly male-like in colour pattern - *i.e.*, non-vittate.

A similar divergence in sexual characteristics has occurred in the apical sinuation of elytra of females of *H. modestus*. Males and females of *H. continentalis* have rounded elytral apices similar to those of male specimens of *H. modestus* (Figs. 7 and 8). Females of *H. modestus*, however, possess an apical sinuation of the elytra (Figs. 9 and 18), possibly allowing distinction between the sexes by the adult beetles.

Position and sclerotization of epipenite (characters 15 and 15, Figs. 4 and 5). – All males of Dytiscinae possess a dorsal sclerite on the male aedoeagus which probably is homologous to the epipenite of male hydaticines. A dorsal positioning of the epipenite therefore would be plesiotypic. A switch to a ventral epipenite among members of certain subgenera of *Hydaticus* could represent a difference in the copulatory function of this sclerite. Correlated to change in position is a trend toward less heavy sclerotization of the epipenite which culminates in its absence from males of *Hydaticinus*.

Width of ventral flange of paramere (character 20, Figs. 14, 27, 35, 42 and 54). – Most males of Dytiscinae do not possess a ventral flange of unsclerotized chitin on the paramere such as is present among hydaticines. This flange, in the apotypic state, is as wide as or wider than the adjacent sclerotized portion of the paramere (Figs. 14, 27 and 35). This state is characteristic of *Hydaticus (s. str.)*.

End-point and terminal width of lateral flanges of median lobe (characters 22 and 23, Figs. 12, 25 and 33). – Most males of Hydaticini possess lateral flanges on the median lobe which taper to a fine point and terminate sub-apically. This represents the plesiotypic state of both characters. Within the species group of *Hydaticus (s. str.)*, which contains Nearctic taxa, these two characters vary in a mosaic pattern (Fig. 58). Both characters have become apotypic independently, however, the combination of apotypic states of both characters (Fig. 12) serves to demonstrate the monophyly of one complex of species.

Hydaticini as a monophyletic unit

All members of Hydaticini examined during this study possess two unique character states which could be interpreted as evidence of a monophyletic assemblage. 1) The suture between the metepisternum and the metasternal wing is straight (Balfour-Browne, 1950, p. 254). 2) A character state which is of great value because of its complexity is the presence, on all males examined, of a possible stridulatory apparatus (Larson and Pritchard, 1974, Figs. 38-42). This apparatus consists of a row of pegs on the tibia (plectrum) opposed to pits on protarsomere 2 (file) (Fig. 1).

Relationships of Higher Taxa of Hydaticini

Proposed relationships of the higher taxa are represented in Fig. 57. Hydaticini are represented by two genera, one of which includes four subgenera.

Adults of *Prodaticus pictus* are markedly plesiotypic. The only proposed synapotypy is that the median lobe is modified from its ancestral form (character 24). This apotypy is unconvincing because deviations from the plesiotypic, parallel-sided shape of the median lobe have taken place many times within Hydaticini and Dytiscinae (group trend). Thus, *P. pictus* appears to represent a taxon little differentiated from the original body plan of Hydaticini, at least, in adult form.

Pleurodytes is a highly autapotypic sister group of *Guignotites* in that they possess a ventrally positioned epipenite and a curved, ventral row of metatibial spines. The latter character is not confined to these subgenera since males of *H.* (*H.*) *cinctipennis* have a slightly curved row of metatibial spines. This curvature is judged to be acquired secondarily in *H. cinctipennis* because in all other characters it is a member of *Hydaticus (s. str.)*.

Franciscolo (1968) inferred that a species group of *Guignotites* centered around *H. leander* Rossi was the most plesiotypic of the entire genus. However, based on the phylogenetic analysis presented, *Guignotites* and *Pleurodytes* should be considered relatively advanced groups of *Hydaticus (s. lat.)*. The *leander* species group is monophyletic, as shown by Franciscolo, because of the lack of a posterior row of bristles on the male protarsal acetabulum. However, this character state must be considered apotypic because the "bristled" state occurs in *Prodaticus* and *Hydaticus (s. str.)*. This interpretation is parsimonious in explaining the complexity of the apex of the median lobe from the simpler forms found in members of *Hydaticus s. str.*, through "bristled" *Guignotites* to the more complex forms among "bristleless" *Guignotites* (compare Figs. 12, 25, 33, 40 and 52 herein to Figs. 96-107 and 119-132 of Franciscolo, 1968).

Relationships of *Hydaticus s. str.*

The reconstructed phylogeny of some of the members of the subgenus *Hydaticus* is shown in Fig. 58. Only a few taxa were available for study, however, at least one monophyletic species group could be defined. Also, a structure is provided on which other taxa can be placed as they become available.

Two major complexes are suggested by the phylogeny: 1) the *cinctipennis-piceus* complex and 2) the *transversalis-semininger-continentalis-modestus* complex. The *cinctipennis-piceus* complex is, perhaps, not monophyletic. In Fig. 58 this complex is isolated from the remainder of the species group on the basis of a colour character and a transformation series. This grouping is maintained in apparent conflict with good structural characters (relative width and length of lateral flanges of the median lobe of the male -- characters 22 and 23). The conflict is supported by correlation with a high degree of autapotypy of *H. cinctipennis* and distribution patterns. These correlations are suggestive of an early isolation of the common stem of *H. cinctipennis* and *H. piceus*.

Male members of the European *H. transversalis* also exhibit a high degree of autapotypy in regard to characters of the aedoeagus. In general facies and elytral colour pattern, this taxon is closely related to the *seminiger-continentalis-modestus* part of the species group. It is possible that *H. transversalis* represents a more recent lineage than the *seminiger-continentalis-modestus* group except that an Upper Miocene fossil has been assigned to this taxon (Galewski and Głazek, 1978).

The *seminiger-continentalis-modestus* group is isolated on the basis of apotypic states of characters 22 and 23. Under "Analysis of Characters" these two characters were presented as varying in a mosaic pattern except in this group where both characters are found in apotypic forms. If the pattern is truly mosaic and is shared only coincidentally by these three taxa, then the group could be paraphyletic.

H. continentalis and *H. modestus* are almost certainly sister species because they are the only taxa belonging to *Hydaticus (s. str.)*, observed to possess vittate elytra. If, however, the ancestral stock of any part of the *transversalis-seminiger-continentalis-modestus* complex can be demonstrated to have possessed vittate elytra then *continentalis* and *modestus* would be grouped on the basis of plesiotypic rather than apotypic character states.

Relationships of *Guignotites*

Most species of *Hydaticus (s. lat.)*, belong to this subgenus and, as such, the complexity of their relationships is outside the scope of this study. American species are few in number, with eight or nine described taxa, as compared to the fauna of other regions -- *e.g.* at least 60 species in the Ethiopian region (Franciscolo, 1968 and Zimmermann, 1920). The understanding of the South American fauna is inadequate and the taxa are so poorly delimited that the formulation of phylogenetic hypotheses is not possible. Characters of possible phylogenetic importance can be gleaned from Franciscolo (1968) and the present study. Preliminary analysis of the available material indicates that the two Nearctic taxa assigned to this subgenus are closely related but a particular species group containing them cannot be discerned.

ZOOGEOGRAPHY

Introduction

Dytiscidae probably arose before the end of the Jurassic (Crowson, 1975). This conclusion comes in part from the position of the family in the Adephaga, which must have been one of the first lineages to have diverged from the remainder of the Coleoptera. As well, many groups of Dytiscidae show gondwanian distribution patterns although subsequent dispersal and vicariance by means of continental movement have obscured some patterns, as have extinctions. A serious problem for zoogeographic interpretation is the lack of phylogenetic analysis of genera and tribes of Dytiscidae. Preliminary analysis of some tribes and genera of Dytiscidae show that a good working hypothesis for dytiscid zoogeography would be one similar to that of Noonan (1979) for anisodactyline carabid beetles.

Some evidence for a gondwanian origin of dytiscids is provided by the observation that most of the Nearctic fauna is derivable from Palaearctic and Neotropical sources (Wolfe, 1979); North America has very few endemic tribes and genera. Matthews (1979) discusses the major routes from Eurasia to North America. One or more of the three North Atlantic routes were probably used by dytiscids during Cretaceous to Eocene times. Invasions from eastern Eurasia were possible via the Bering land bridge which is thought to have existed at sporadic intervals from Cretaceous through Pleistocene times (Matthews, 1979).

Faunal affinities to the Neotropical realm indicate that a number of lineages have entered North America from the south. These invasions have probably come about after one of the many closures of the Panamanian portal which range in age from late Pliocene to the present (Childs and Beebee, 1963).

General Patterns of Distribution

Two of the five higher taxa [*Prodacticus* and *H.* (*Pleurodytes*)] considered in this study are confined to small areas within the Oriental region, and another [*H.* (*Hydaticinus*) from Argentina north to Trinidad] to the Neotropical realm. Presence of both relict, plesiotypic, and apotypic taxa, as well as the greatest diversity of Hydaticini in the Palaeotropics leads to the hypothesis that Hydaticini have arisen and diversified on the continental land mass of Africa when that continent was part of Gondwanaland. Africa represents the zoogeographic centre from which taxon "pulses" (Erwin, 1979) have originated. These "pulses" represent forms capable of rapid colonization of new areas presumably because of entering a new adaptive zone which has allowed them to out-compete the established inhabitants if any were present. The first "pulse" of Hydaticini could have given rise to *Prodaticus* which could have dispersed from Africa into the Oriental region where it is found today. The next "pulse" is represented by *Hydaticus (s. str.)*, which could have replaced *Prodaticus* in Africa first and secondly in the

Palearctic region as the former taxon began to colonize that area. Subsequently, *Hydaticus (s. str.).* was replaced in the tropics by the more advanced *Guignotites* as the latter began to diversify.

Distribution of *Hydaticus (s. str.)* in North America

Hydaticus (s. str.), is primarily Holarctic in distribution. The three species of *Hydaticus (s. str.)* in the Nearctic Region are of quite different ages. *H. modestus* is a recent arrival whereas *H. piceus* and *H. cinctipennis* represent much older invasions.

The common ancestor of *H. piceus* and *H. cinctipennis* probably entered North America from western Eurasia. The most plausible route would seem to be one of the three North Atlantic routes discussed by Matthews (1979) ranging in age from Cretaceous to Eocene (Figs. 58 and 60). The *H. cinctipennis-piceus* ancestor having entered North America diverged into the two extant taxa. A North Atlantic route for the common ancestor of these two species is suggested by their present distributions. The two species are confined to the eastern U.S.A., and the Atlantic and Gulf Coastal distribution of *H. cinctipennis* represents a relict distributional pattern. The vicariant event which most likely came to separate *H. cinctipennis* and *H. piceus* was the fluctuation of epicontinental seas in the southeastern United States in the Pliocene and Pleistocene (Howden, 1963). Ancestral *H. cinctipennis* was isolated in central Florida by marine transgressions whereas the ancestral *H. piceus* was diverging on the remainder of the continent to the north of the seaway. This reconstruction presupposes that *H. piceus* and *H. cinctipennis* represent a monophyletic grouping. Further information on the phylogeny of *Hydaticus (s. str.)*, will be of great value in testing the zoogeographic hypothesis.

The second invasion of North America by *Hydaticus (s. str.)*, is represented by *H. modestus*, a relatively recent species (Figs. 58 and 60). One clue which suggests that *H. modestus* is recent is its widespread distribution which is characteristic of more recent taxa. This species, derived from a common ancestor of it and *H. continentalis*, entered North America by means of the Bering land bridge possibly as late as the Pleistocene. The vicariant event which separated the two taxa was probably been eustatic, sea-level fluctuation which led to sporadic closings of the Bering land bridge.

Once *H. modestus* entered North America something can be deduced of its recent history from distribution of its two female elytral morphs (Fig. 19). Analysis of distribution of "rugose" and "smooth" elytral sculpture implies two different full-glacial Wisconsin refugia. These are the Beringian refugium for the rugose form and the eastern-deciduous forest refugium for the smooth form (Fig. 59A). Post-glacial warming and retreat of ice northward would have allowed the smooth form to colonize North America in a westward direction whereas the Beringian population remained isolated in northwestern North America (Fig. 59B). This Beringian population presumably became adapted to a shorter growing season and developed rugose elytra of females. In post-glacial times this Beringian morph has colonized those areas of North America with continental type climates whereas the smooth morph has predominated in more temperate areas.

Distribution of *Guignotites* in North America

As mentioned above, under the Relationships of *Guignotites*, phylogeny of this subgenus is quite involved and complicated. The fauna within the Americas is only a very small part of the total fauna, members of which occur world-wide. A preliminary analysis shows the American fauna to represent a plesiotypic level within *Guignotites* which can be interpreted as indicating that *Guignotites* was present in South America before that continent separated from Africa. Members of *Guignotites* occurring in North America would then represent a northward extension of the Neotropical fauna after one of the many closures of the Panamanian portal. This zoogeographic hypothesis will be tested as further knowledge is gained about phylogeny of the subgenus. For instance, the hypothesis would be disproved if the North American *Guignotites* are not closely related to the South American *Guignotites* or if the South American *Guignotites* are not representative of a gondwanian colonization of South America.

If the common ancestor of *H. bimarginatus* and *H. rimosus* did enter North America after the closure of the Panamanian portal then they probably represent a vicariant species pair. Both species have an affinity for forest-pond situations and therefore a vicariant event such as development of a grassland barrier between the southeastern United States (*H. bimarginatus*) and Mexico (*H. rimosus*) in the Miocene (Martin and Harrell, 1957; Rosen, 1978; and Allen and Ball, 1980), could have brought about the speciation. This hypothesis would require that the Caribbean islands were colonized secondarily after the speciation event. Another hypothesis would be that speciation took place in Central America by means of one of the events described by Rosen (1978) and that *H. bimarginatus* has colonized southeastern United States by means of island-hopping across the Caribbean. This hypothesis seems less likely because of the absence of *H. bimarginatus* from critical staging points such as Jamaica. The island-hopping is invoked, however, to explain the presence of *H. rimosus* in Cuba although it is also absent from Jamaica but it is present in other critical staging areas such as the Yucatan Peninsula. A summary of the zoogeographic and phylogenetic relationships of North American *Guignotites* is shown in Fig. 60.

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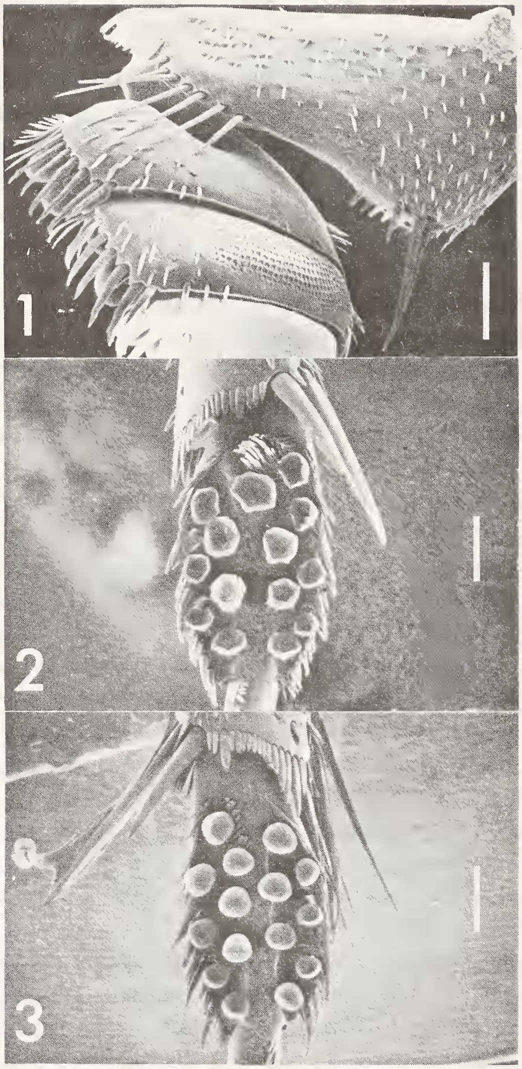
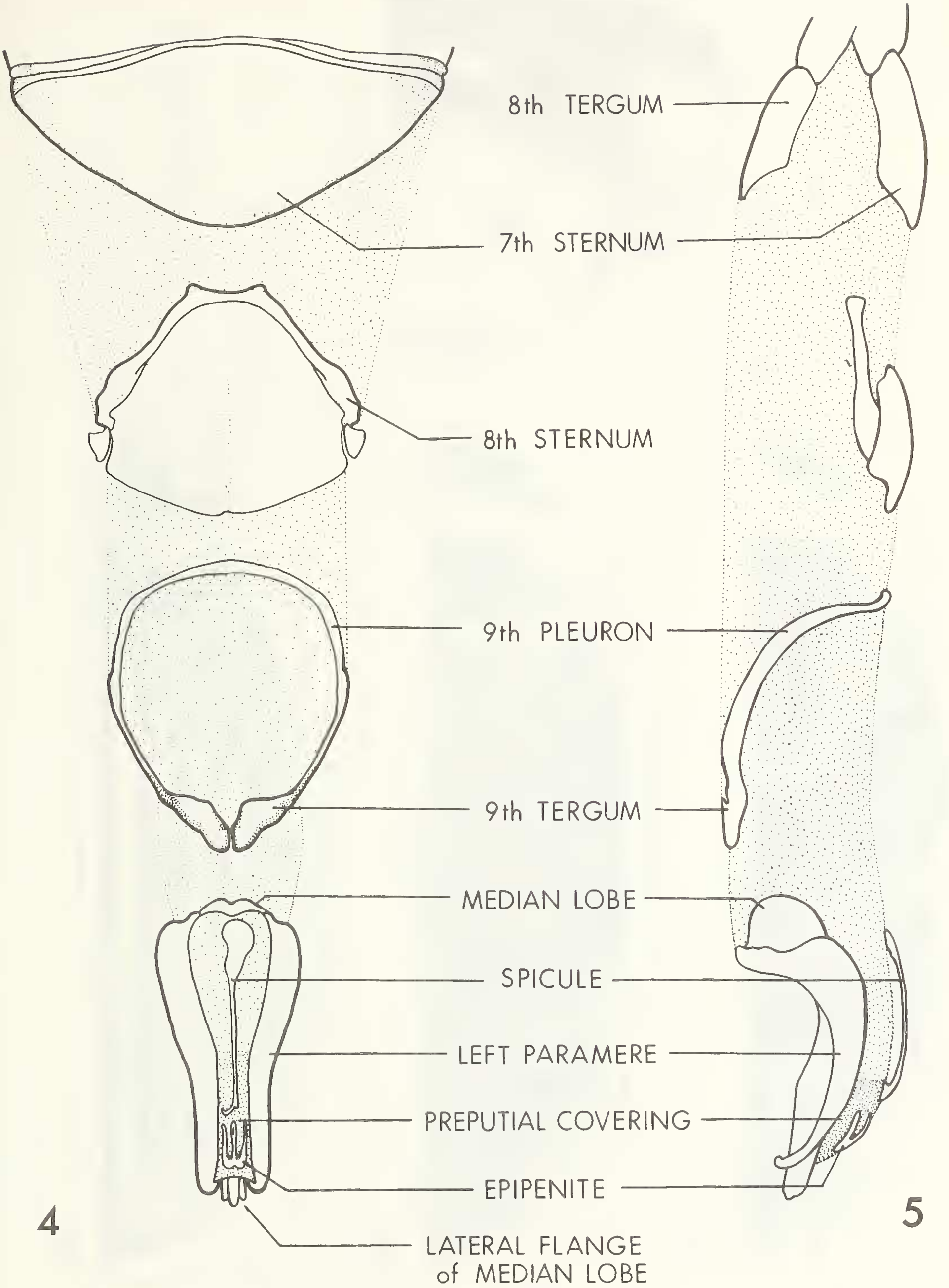
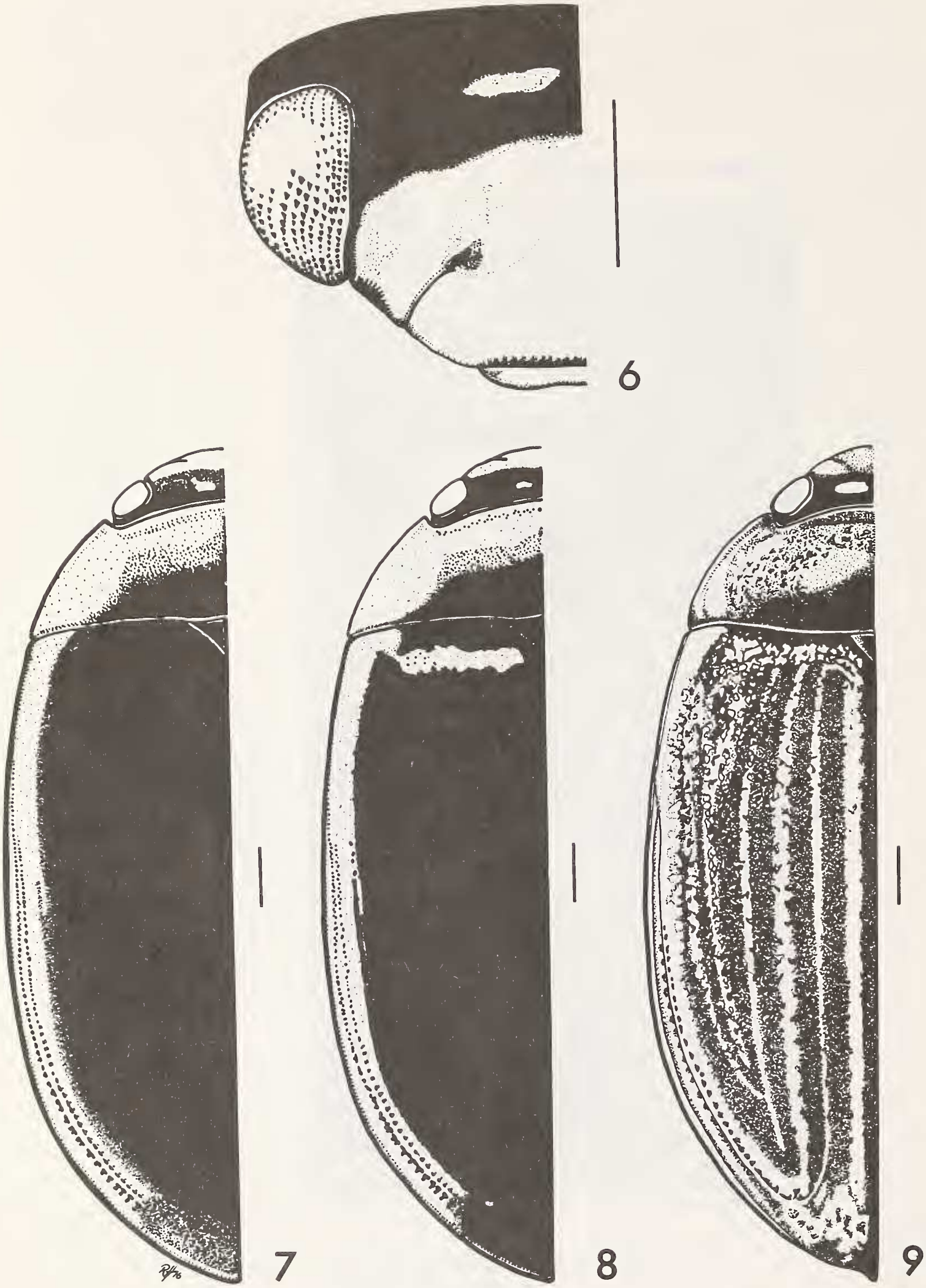


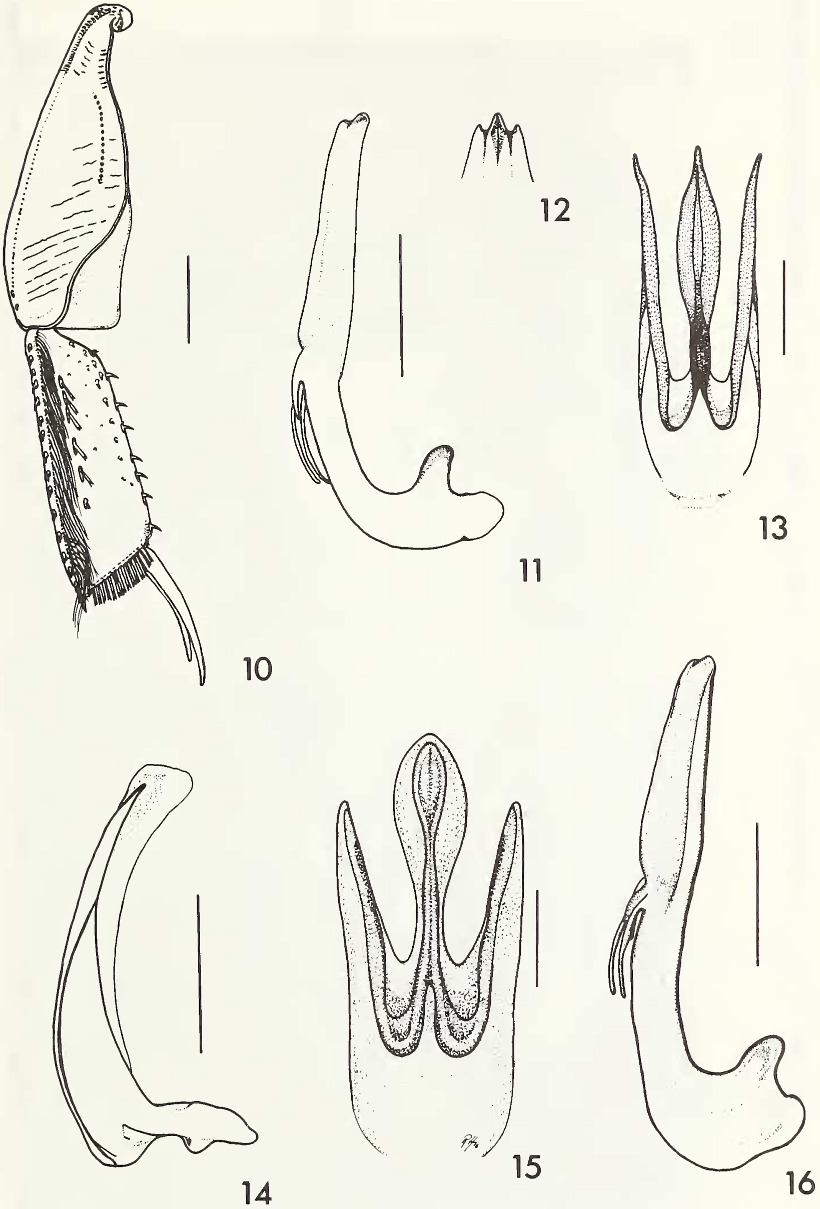
Figs. 1 and 2. *Hydaticus* (*Hydaticus*) *piceus* LeConte. Scanning electron micrographs. Fig. 1. Protarsus and protibia of male specimen in anterolateral view. Fig. 2. Three basal segments of male mesotarsus in ventral view. Fig. 3. *Hydaticus* (*Guignotites*) *rimosus* Aubé. Three basal segments of male mesotarsus in ventral view.



Figs. 4 and 5. Genital appendages of male of *Hydaticus* (*Hydaticus*) *modestus* Sharp. Fig. 4. Ventral view. Fig. 5. Lateral view.

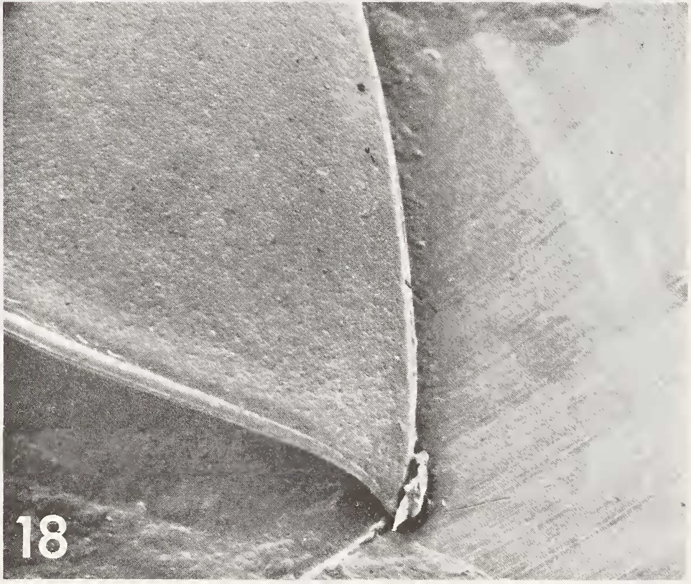


Figs. 6 to 9. Parts of the body of *Hydaticus* (*Hydaticus*) *modestus* Sharp. Fig. 6. Right half of head. Left half of body in dorsal view, illustrating: Fig. 7. Non-fasciate elytron. Fig. 8. Fasciate elytron. Fig. 9. Vittate elytron.



Figs. 10 to 14. Parts of the body of *Hydaticus* (*Hydaticus*) *modestus* Sharp. Fig. 10. Left metafemur and metatibia, posterior surfaces. Fig. 11. Median lobe of aedoeagus, side view. Fig. 12. Median lobe of aedoeagus, ventral view of apex. Fig. 13. Epipenite of aedoeagus. Fig. 14. Left paramere of aedoeagus. Figs. 15 and 16. Parts of the aedoeagus of *Hydaticus* (*Hydaticus*) *continentalis* J. Balfour-Browne. Fig. 15. Epipenite. Fig. 16. Median lobe, side view.


17


18

Figs. 17 and 18. Scanning electron micrographs of elytron of a female of *Hydaticus* (*Hydaticus*) *modestus* Sharp. Fig. 17. Rugose elytron. Fig. 18. Sinuate apex of elytron.

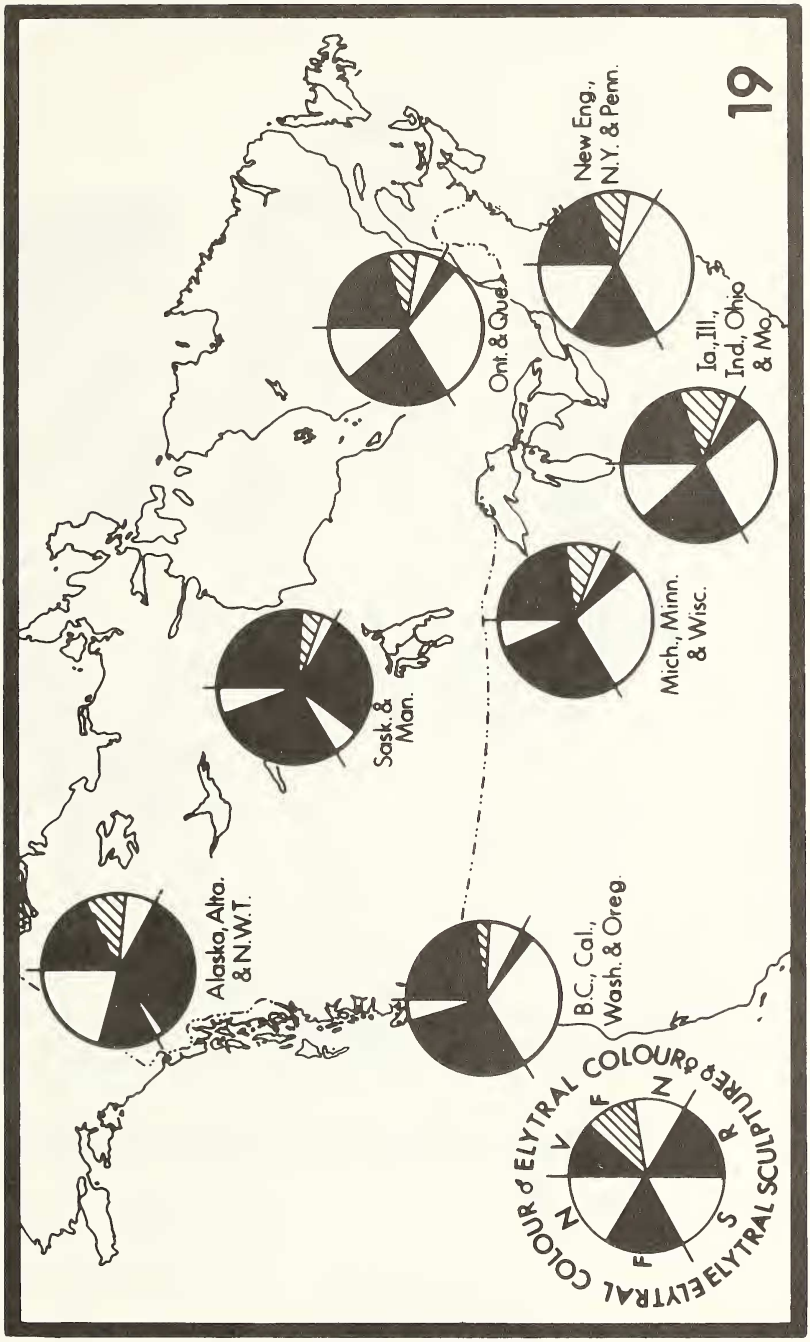


Fig. 19. Geographic distribution of certain elytral characteristics of selected samples of specimens of *Hydaticus* (*Hydaticus*) *modestus* Sharp.

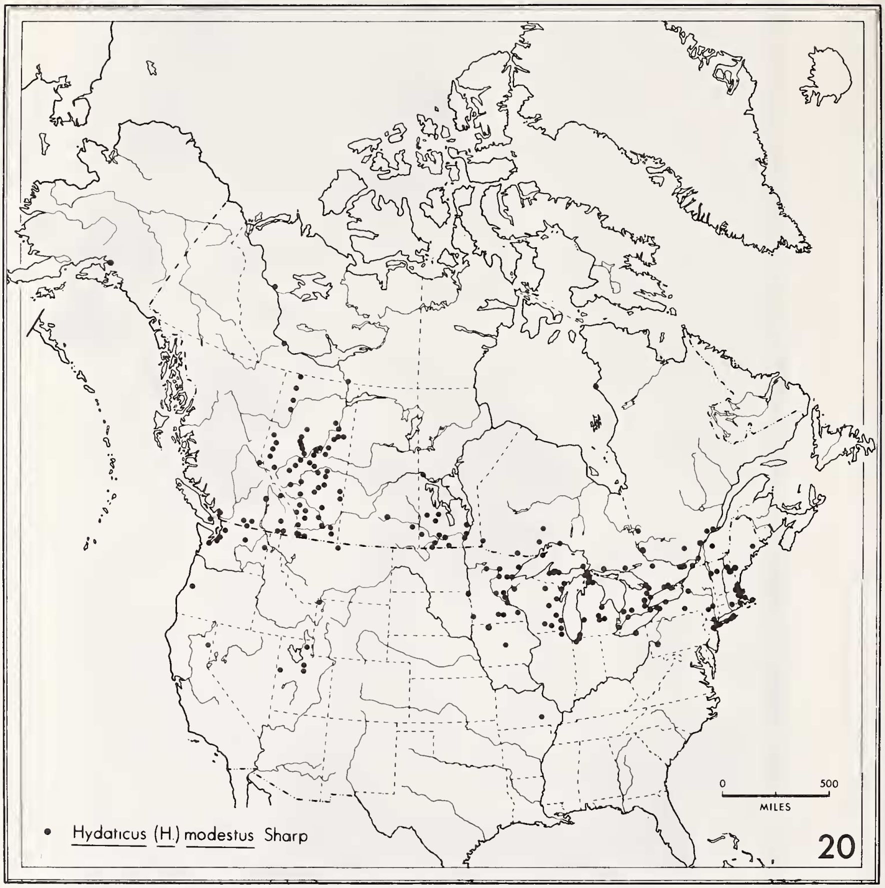
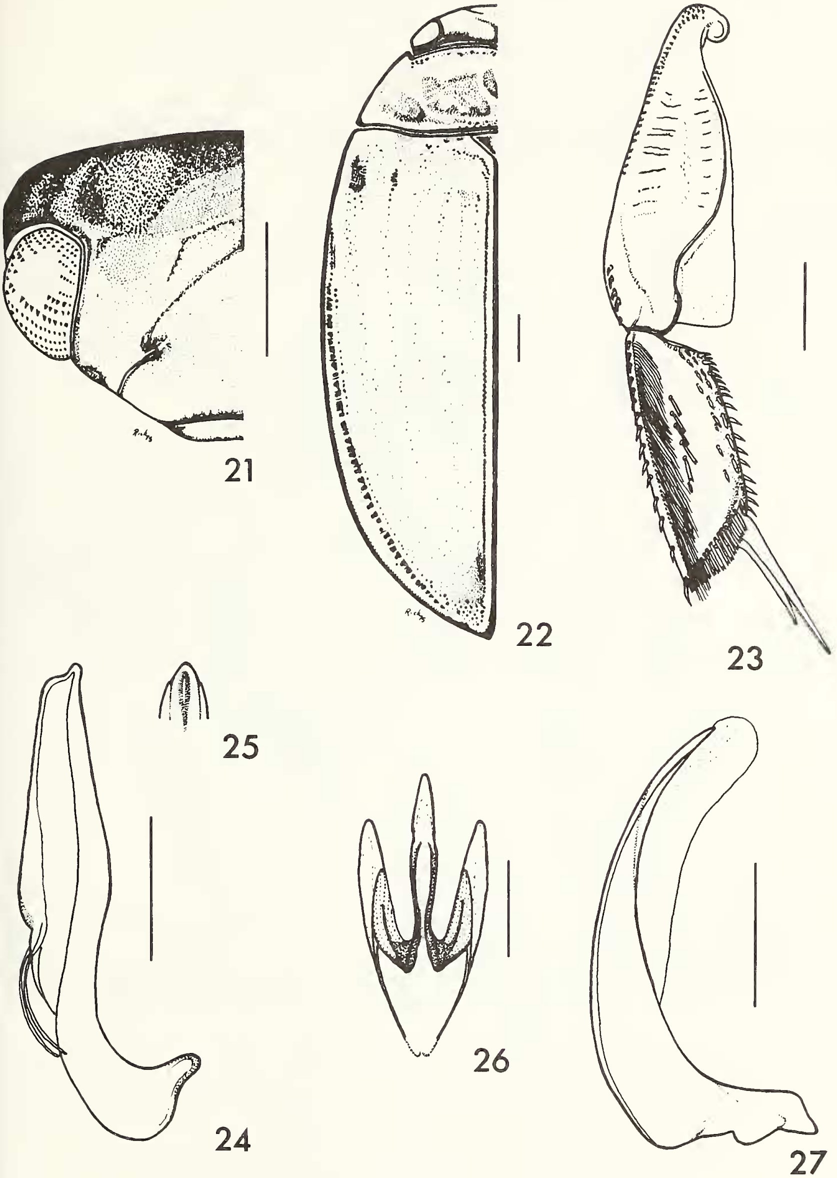
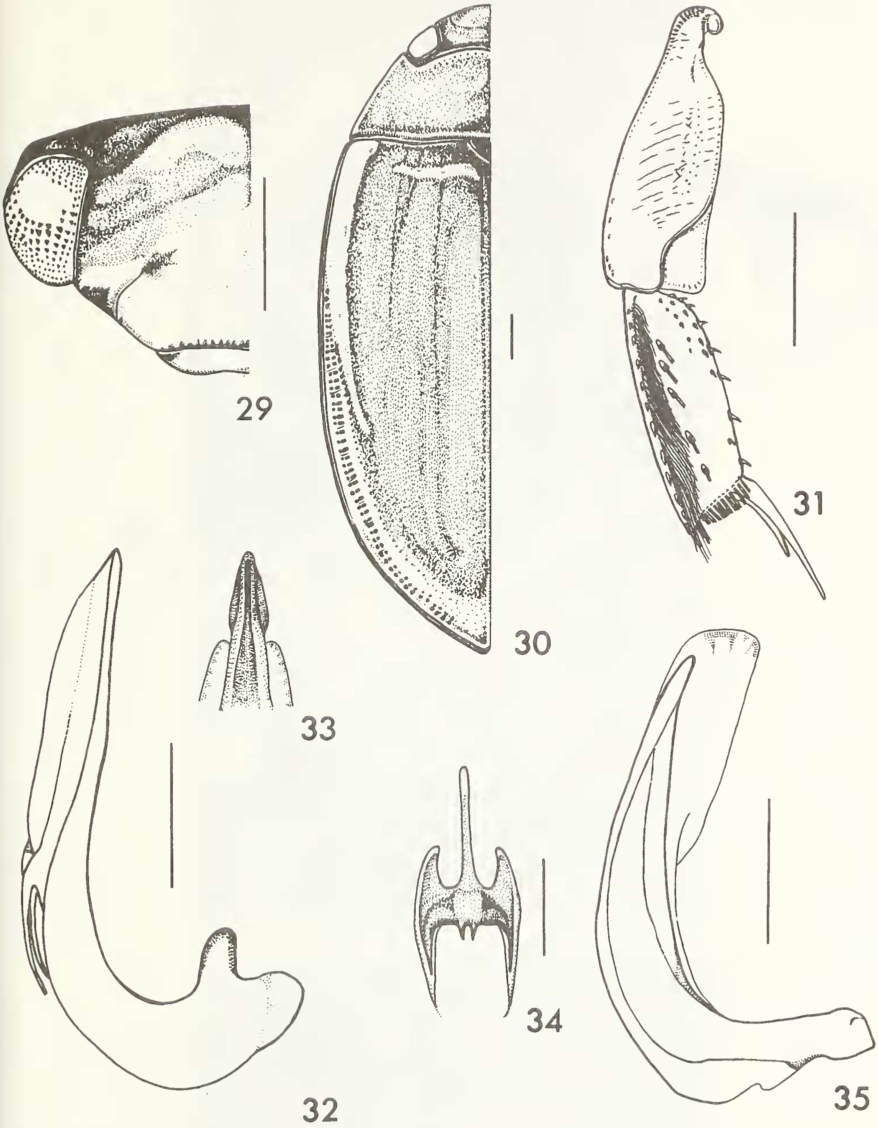


Fig. 20. Distribution of *Hydaticus* (*Hydaticus*) *modestus* Sharp, within North America.

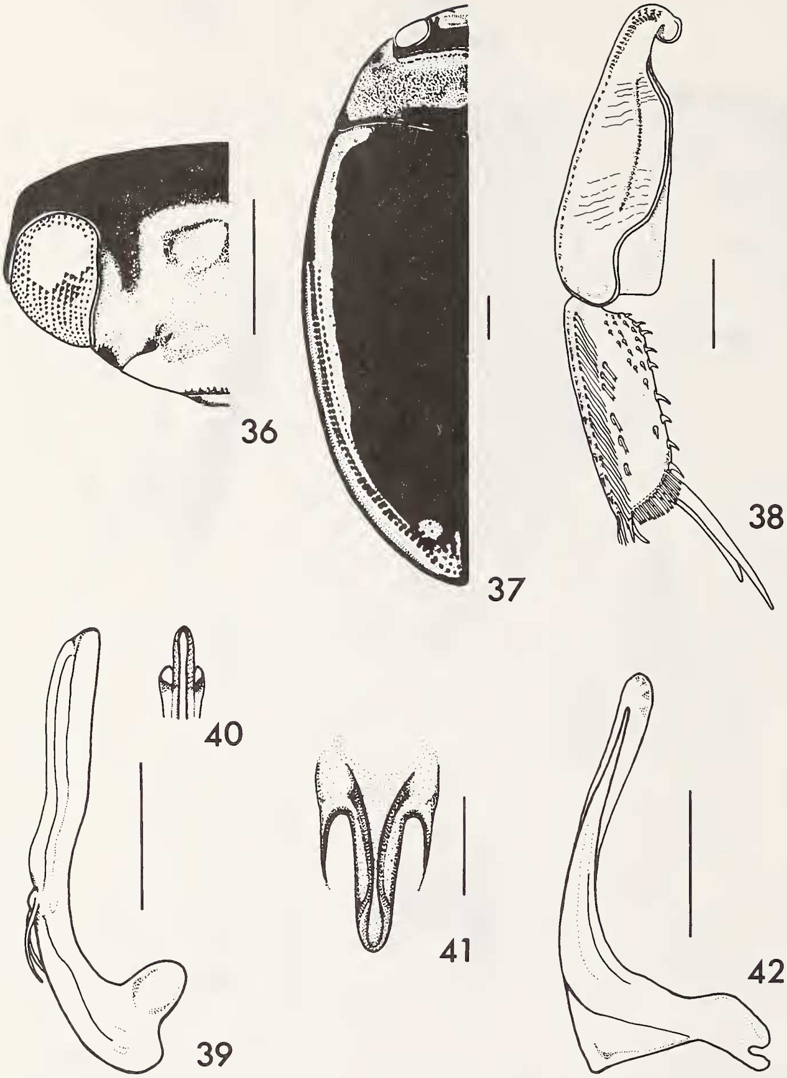


Figs. 21 to 27. Parts of the body of *Hydaticus* (*Hydaticus*) *piceus* LeConte. Fig. 21. Right half of head. Fig. 22. Left half of body. Fig. 23. Left metafemur, and metatibia, posterior surfaces. Fig. 24. Median lobe of aedoeagus, side view. Fig. 25. Median lobe of aedoeagus, ventral view of apex. Fig. 26. Epipenite of aedoeagus. Fig. 27. Left paramere of aedoeagus.

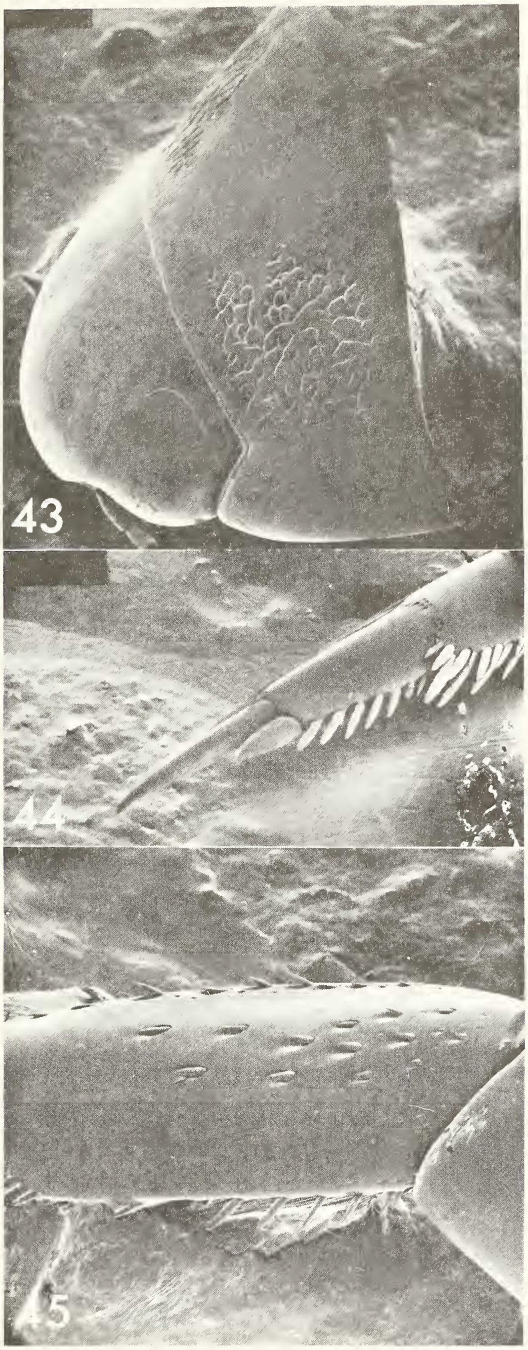
Fig. 28. Distribution of *Hydaticus* (*Hydaticus*) *cinctipennis* Aubé, and *Hydaticus* (*Hydaticus*) *piceus* LeConte.



Figs. 29 to 35. Parts of the body of *Hydaticus* (*Hydaticus*) *cinctipennis* Aubé. Fig. 29. Right half of head. Fig. 30. Left half of body. Fig. 31. Left femur and metatibia, posterior surfaces. Fig. 32. Median lobe of aedoeagus, side view. Fig. 33. Median lobe of aedoeagus, ventral view of apex. Fig. 34. Epipenite of aedoeagus. Fig. 35. Left paramere of aedoeagus.

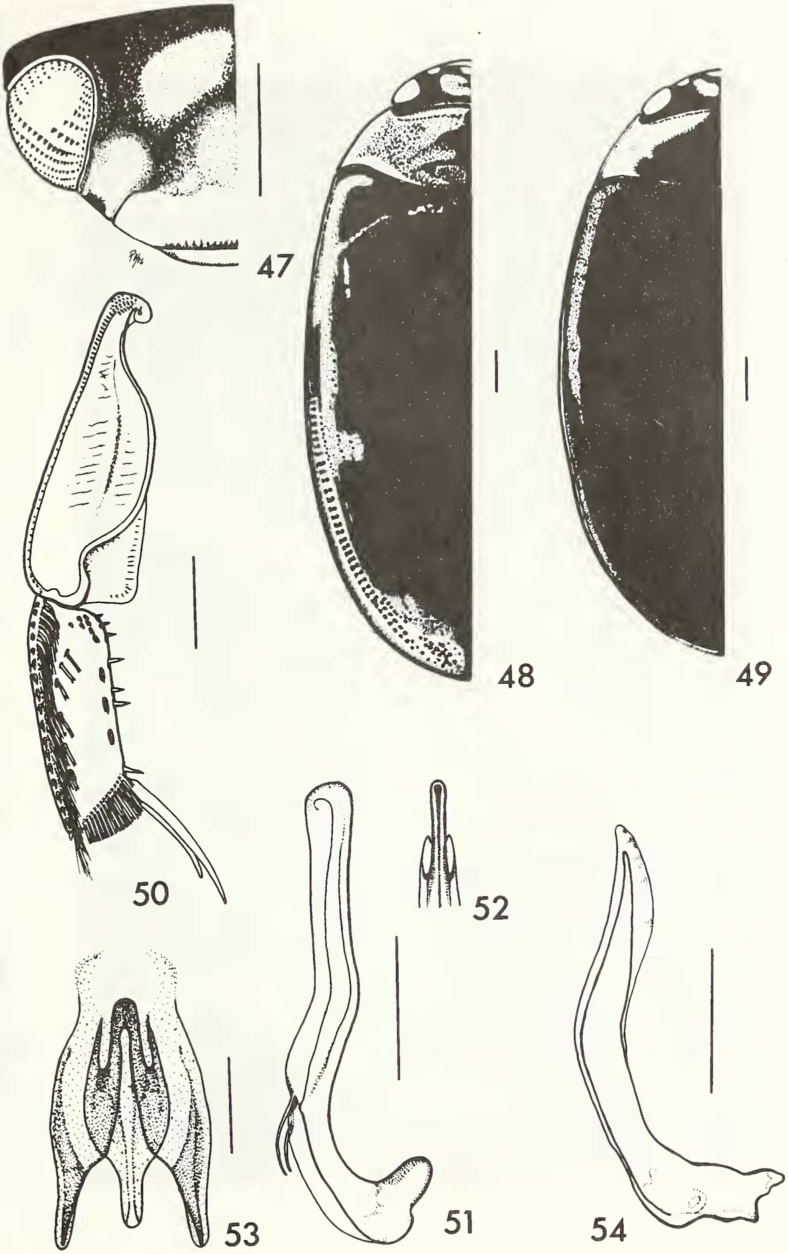


Figs. 36 to 42. Parts of the body of *Hydaticus* (*Guignotites*) *bimarginatus* (Say). Fig. 36. Right half of head. Fig. 37. Left half of body. Fig. 38. Left metafemur, and left metatibia, posterior surfaces. Fig. 39. Median lobe of aedoeagus, side view. Fig. 40. Median lobe of aedoeagus, ventral view of apex. Fig. 41. Epipenite of aedoeagus. Fig. 42. Left paramere of aedoeagus.

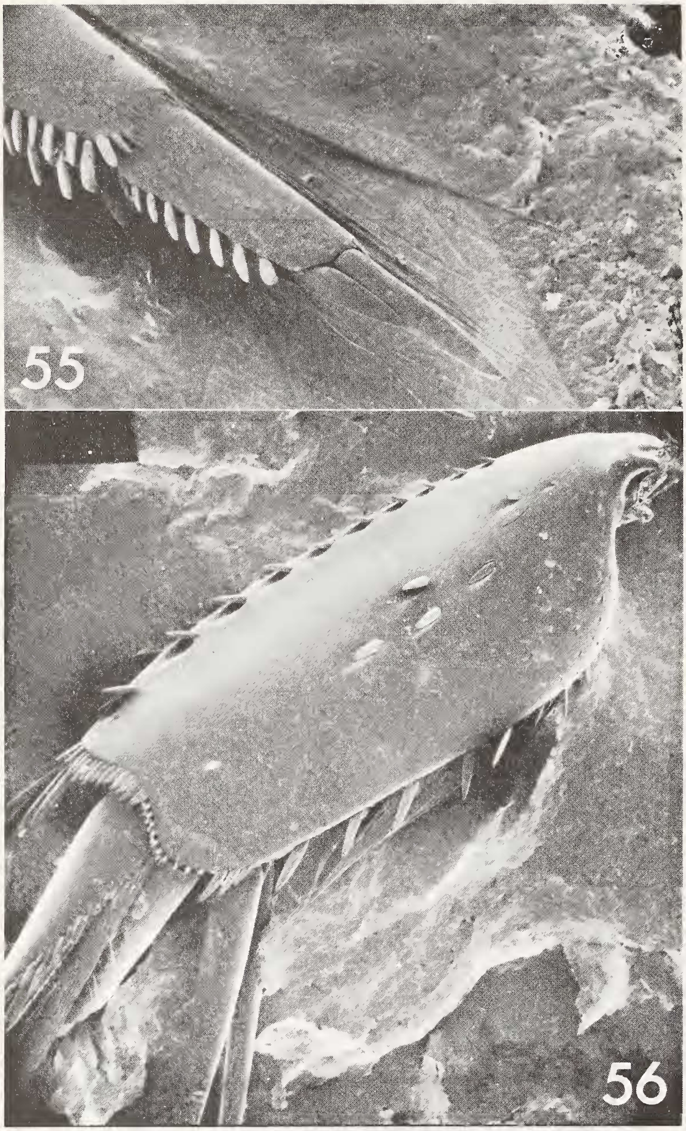


Figs. 43 to 45. Scanning electron micrographs of *Hydaticus* (*Guignotites*) *bimarginatus* (Say). Fig. 43. Head and pronotum of female. Fig. 44. Metatarsal claws of male. Fig. 45. Disc of metatibia, anterior surface, of male, showing 13 large spines.

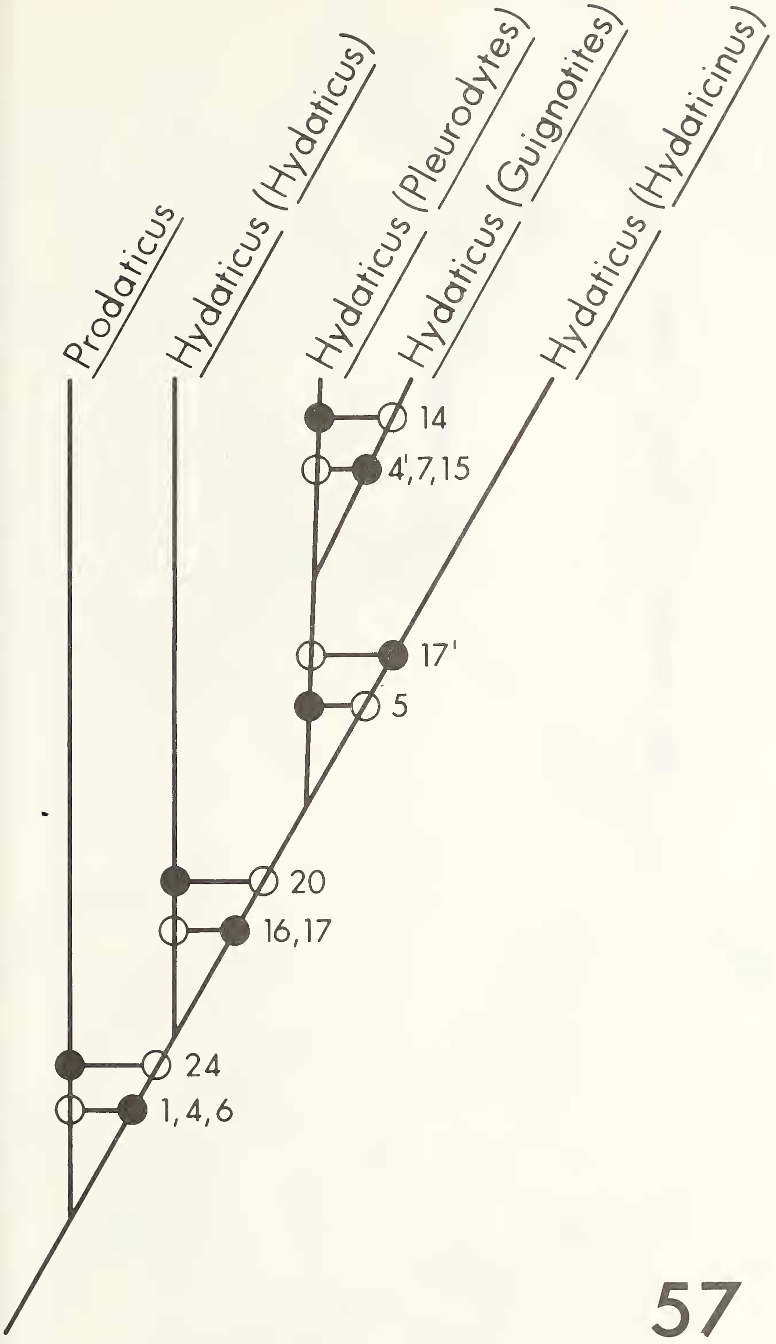
Fig. 46. Distribution of *Hydaticus* (*Guignotites*) *bimarginatus* (Say), and *Hydaticus* (*Guignotites*) *rimosus* Aubé.



Figs. 47 to 54. Parts of the body of *Hydaticus (Guignotites) rimosus* Aubé. Fig. 47. Right half of head. Fig. 48. Left half of body. Fig. 49. Left half of body. Fig. 50. Left metafemur, and left metatibia, posterior surfaces. Fig. 51. Median lobe of aedoeagus, side view. Fig. 52. Median lobe of aedoeagus, ventral view of apex. Fig. 53. Epipenite of median lobe. Fig. 54. Left paramere of aedoeagus.

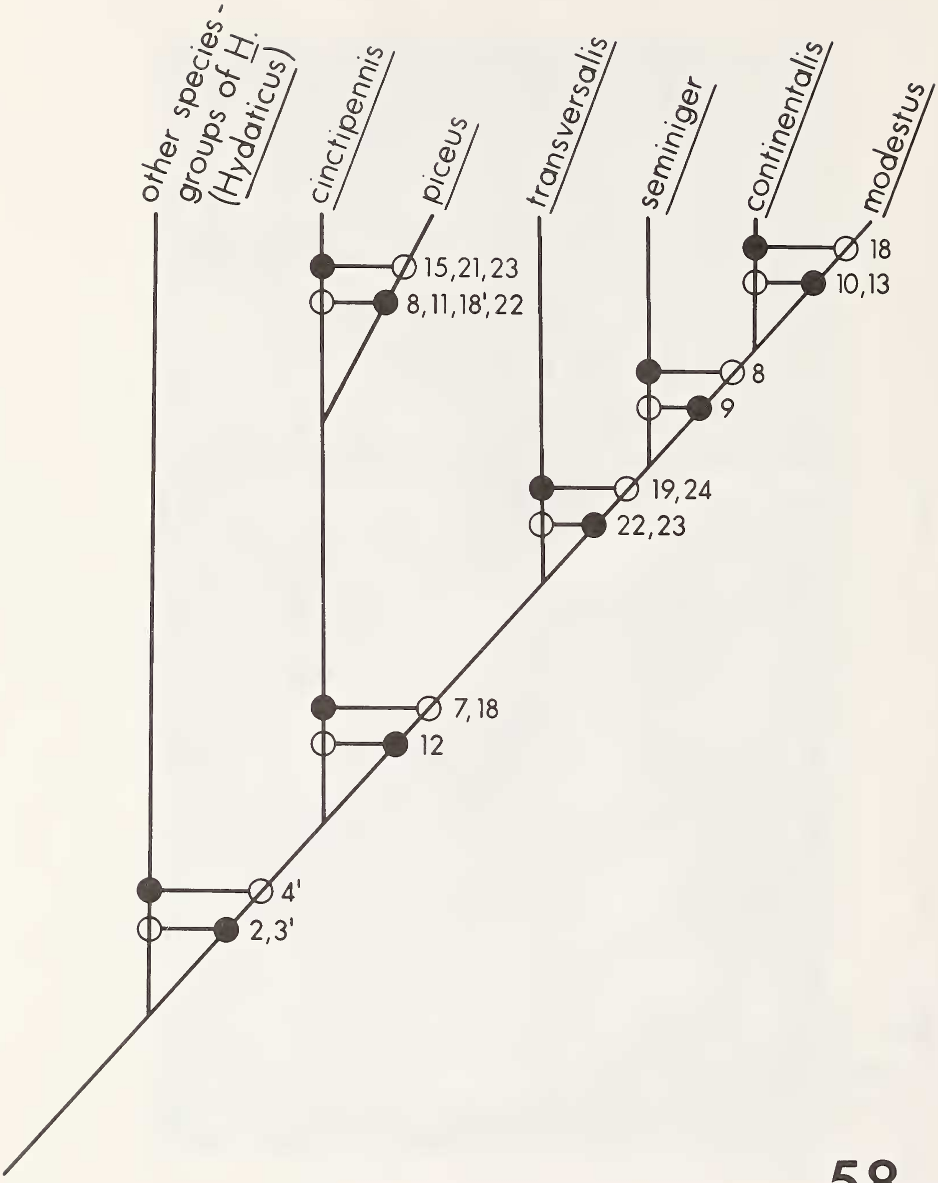


Figs. 55 and 56. Scanning electron micrographs of *Hydaticus* (*Guignotites*) *rimosus* Aubé. Fig. 55. Metatarsal claws. Fig. 56. Disc of metatibia, anterior surface, showing 5 large spines.



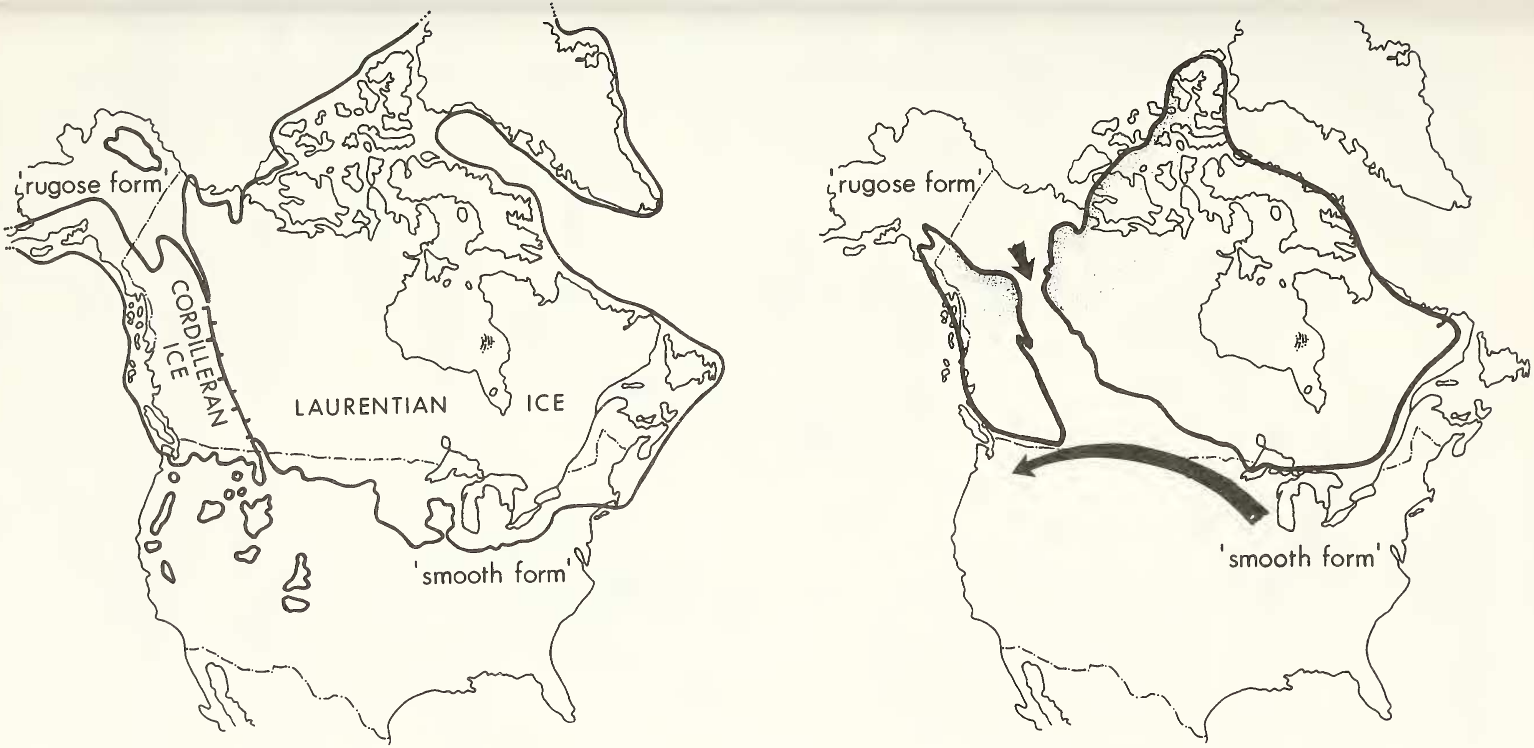
57

Fig. 57. Reconstructed phylogeny of the higher taxa of Hydaticini. Open circles represent the plesiomorphic, filled circles the apomorphic states presented in Table 4.



58

Fig. 58. Reconstructed phylogeny of the species-group of *Hydaticus* (*Hydaticus*) which contains North American taxa. Open circles represent the plesiomorphic, filled circles the apomorphic states presented in Table 4.



59A

59B

Fig. 59. Zoogeographic derivation of pattern of distribution of smooth and rugose forms of elytral sculpture of females of *Hydaticus* (*Hydaticus*) *modestus* Sharp. Fig. 59A. Maximum distribution of glacial ice in North America at the peak of Wisconsin glaciation (after Nimmo, 1971, fig. 664). At this time the rugose form was within the Beringian refugium and the smooth form in the eastern-deciduous forest refugium. Fig. 59B. Approximate ice positions at about 11,000 years before present (after Prest, 1969). During retreat of ice sheets the smooth form dispersed westward whereas the Beringian population remained isolated. Later the Beringian, rugose form colonized central North America to achieve the present distribution shown in Fig. 19.

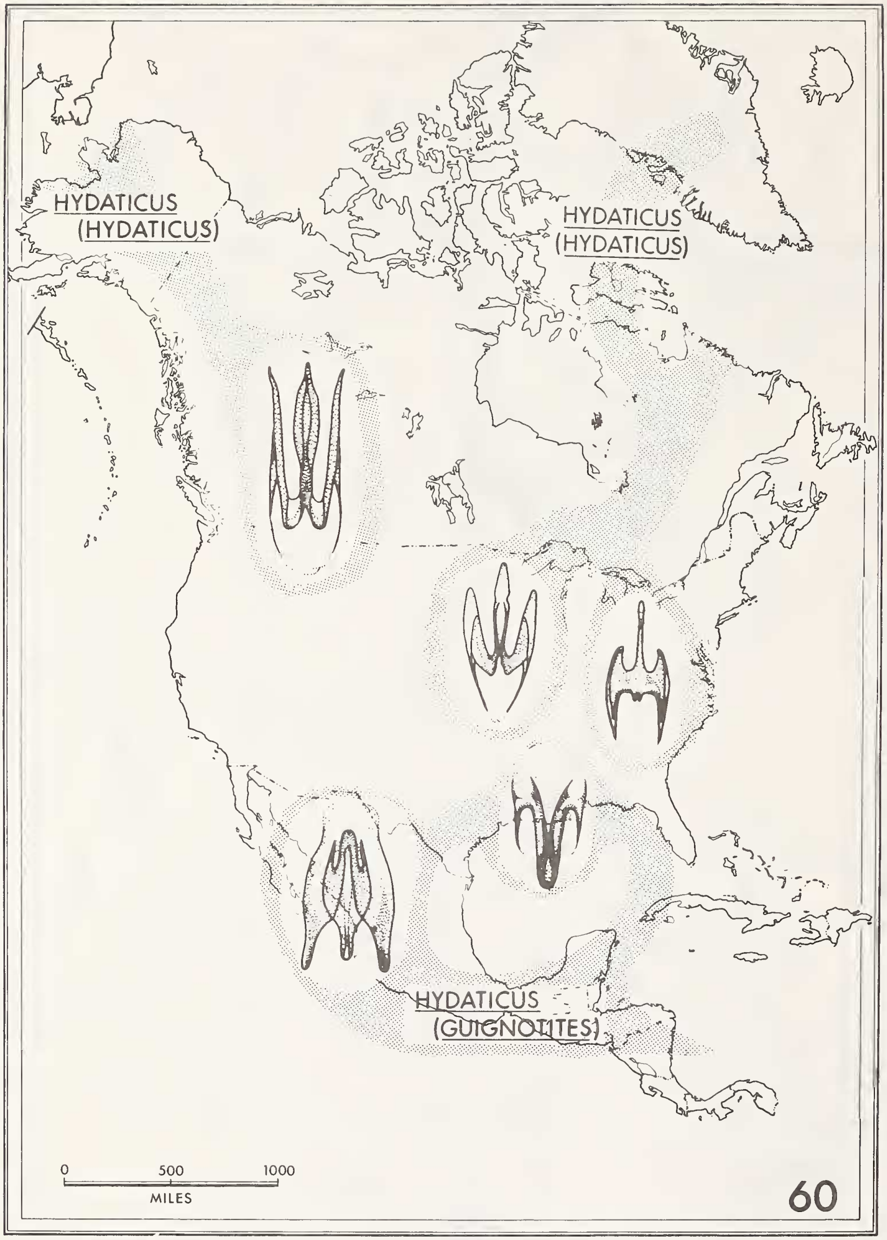


Fig. 60. Summary of the phylogenetic and zoogeographic relationships of North American *Hydaticus*. The epipenite of the aedoeagus of the male is used as a pictorial representation of species. The subgenus *Hydaticus* has probably had two separate invasions of North America and the subgenus *Guignotites* has possibly only invaded once.

Index to Names of Taxa